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New Directions in Island Biogeography

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Abstract

Aim: Much of our current understanding of ecological and evolutionary processes comes from island research. With increasing availability of data on distributions and phylogenetic relationships, and new analytical approaches to understanding the processes that shape species' distributions and interactions, a prospective on this ever-interesting topic is timely.

Location: Islands globally.

Methods: We start by arguing that the reasons island research has achieved so much in the past also apply to the future. We then critically assess the current state of island biogeography, focusing on recent changes in emphasis, including research featured in this special issue of *Global Ecology and Biogeography*. Finally, we suggest promising themes for the future. We cover both ecological and evolutionary topics, although the greater emphasis on island ecology reflects our own backgrounds and interests.

Results: Much ecological theory has been directly or indirectly influenced by research on island biotas. Currently, island biogeography is renascent, with research focusing on, among other things, patterns and processes underlying species interaction networks, species coexistence and the assembly of island communities through ecological and evolutionary time. Continuing island research should provide additional insight into biological invasions and other impacts of human activities, functional diversity and ecosystem functioning, extinction and diversification, species pools and more. Deeper understanding of the similarities and differences between island and mainland systems will aid transferability of island theory to continental regions.

Main conclusions: As research in biogeography and related fields expands in new directions, islands continue to provide opportunities for developing insights, both as natural laboratories for ecology and evolution and because of the exceptions islands often present to the usual 'rules' of ecology. New data-collection initiatives are needed on islands worldwide and should be directed towards filling gaps in our knowledge of within-island distributions of species, as well as island species' functional traits and phylogenetic relationships.

Introduction

"In islands we have the facts of distribution often presented to us in their simplest forms, along with others which become gradually more and more complex; and we are therefore able to proceed step by step in the solution of the problems they present."

(Wallace, 1880, p. 234)

The nature of island biology research

Wallace (1880) argued that islands offer solutions to key 'problems' in biogeography, ecology, and evolutionary biology. But do biologists still believe this? Or has island biogeography become peripheral to the mainstream, pursued by a few enthusiasts mindful of early seminal contributions of island studies to these fields? Do islands continue to provide key insights and unique settings for research on important biogeographical, ecological, and evolutionary questions? We argue here that the answer to the last question is emphatically "yes". While island-specific knowledge and understanding continue to grow, island biogeography is more integrated with mainstream research than ever before, and this integration will intensify over the coming decades.

Current themes in ecology, biogeography and evolutionary biology include the causes of variation in species richness, the assembly of ecological communities, mechanisms shaping the outcomes of evolutionary processes (including adaptive radiations), and the impact of global change on biodiversity (e.g. Sutherland *et al.*, 2013). These issues are complex, involving scale-dependent processes, including species interactions, dispersal and colonization, gene flow and population dynamics, all played out in a heterogeneous world. Addressing such broad and complex issues will require the resolution of underlying mechanisms into straightforward hypotheses amenable to testing by experimental or comparative approaches. Islands can be powerful allies in such endeavours.

Island systems often present ecological, evolutionary and geological processes on timescales (usually so different among these processes) that are relatively similar, and often quite recent. On volcanic oceanic islands (Box 1), in particular, geological dynamics may be unusually fast and ecological dynamics relatively slow, aligning both quite closely with each other and with evolutionary dynamics (Rominger *et al.*, this issue). Spatial scales tend to be compressed (e.g., by steep terrain) and spatial structure within archipelagos is discrete; local extinctions on oceanic islands are often global extinctions; and population differentiation between and within islands provides model systems for studying speciation. These features of islands provide a valuable testing ground for theory because they break typical scaling relationships that constrain the expression of many key biological processes within larger continental regions (Warren *et al.*, 2015).

The importance of islands thus goes far beyond their shorelines and, ever since the seminal works of the great nineteenth century naturalists, much of the understanding gained from island-based studies has informed studies of mainland systems, as illustrated by many of the references highlighted in Tables 1 and S1. Indeed, during the 19th century, the work of Charles Darwin in the Galápagos Archipelago and of Alfred Russel Wallace in the Malay Archipelago, secured island biology in the foundation of contemporary research across most biological disciplines. Much of our current understanding of the ecological and evolutionary processes that shape diversity patterns comes from knowledge gained from islands. As Robert MacArthur and Edward O. Wilson (1967: 3) stated, "insularity is … a universal feature of biogeography … many of the principles graphically displayed in the Galápagos Islands … apply in lesser or greater degree to all natural habitats." Some discrete

habitats have been studied in the context of island theory, from mountaintops (or 'sky islands') to forest fragments and lakes (e.g. Brown, 1971, 1978; March & Bass, 1995), and island theory has provided the conceptual basis for much research on the ecological impacts of habitat fragmentation (Laurance, 2009). Island-like marine environments (e.g., marine lakes, i.e. pieces of seawater entirely surrounded by land; seamounts) also can be integrated within the general theories of island biogeography, according to Dawson (this issue). More generally, insularity within the contiguous landmasses of the continents remains under-appreciated (but see Steinbauer *et al.*, in press b), and the same may apply to the oceans.

In their 'equilibrium theory of island biogeography' (ETIB; Box 1), MacArthur and Wilson (1963, 1967) applied insights from the population biology of the early-mid 20th century (birth and death processes) to island biogeography (colonization and extinction), and then to other disciplines (e.g., conservation biology). As well as leading to a paradigm shift within island research, this theory played a central role in the development of conservation theory (Pimm, 1991) and was a starting point for Hubbell's (2001) development of the neutral theory of ecology.

Other theories and models that developed out of island research have become mainstays of ecology, conservation, and biogeography, sometimes with their island origins obscured (Tables 1, S1). The role of competition in patterns of species' occurrences across archipelagos, the subject of sometimes acrimonious debate in the 1970s (e.g. Diamond, 1975; Connor & Simberloff, 1979), revitalized interest in studying mechanisms of community assembly (Simberloff & Collins, 2009). The 'assembly rules' (Box 1) debate also led to the current emphasis on formulating appropriate null models for community assembly (e.g. Weiher & Keddy, 1995), entailing the use of randomized null simulations for interpreting empirical results in biogeography (stemming from Connor & Simberloff, 1979; Gotelli & Graves, 1996). Further, the controversy raised by Jared Diamond's (1975) analysis of the mechanisms of community assembly can be linked to Hubbell's (2001) 'unified neutral theory of biodiversity and biogeography'. Hubbell developed this theory "on the foundation of the ETIB" (Hubbell, 2001: 5), being partly based on the randomness of colonization and extinction of the ETIB, also by setting local communities in a geographical metacommunity, as islands are embedded in a colonization landscape. However, Hubbell defined neutrality at the individual level, with species being equivalent within a trophic guild and species' abundance and diversity in a community being determined by random individual birth, death, and dispersal events. He also added a speciation term, using a model of random species formation. Hubbell's theory can reproduce a wide range of community and biogeographic patterns, and it has initiated continuing debate on the nature of a world without ecological interactions (Ricklefs, 2006; Leigh, 2007; Rosindell *et al.*, 2011).

We should also remember that Wright's (1983) species–energy theory, the impact of which has mainly been in research on the causes of the latitudinal gradient in biodiversity, stems from island research. Wright developed his theory as an extension of the ETIB, particularly its species–area component, amalgamating it with Brown's (1981) focus on energetics (see also Brown *et al.*, 2004). The simple replacement of 'area' by 'available energy' in the ETIB, combined with Preston's (1962a, b) earlier model for the distribution of species' abundances, focused attention on relationships between energy availability and population sizes, extinction rates, and species richness. Similarly, Rosenzweig (1975) reformulated ETIB for continental regions, replacing immigration with species formation.

Amid the excitement about the value of islands for understanding the world in general, islands clearly are interesting in their own right. Islands are home to some of the most bizarre and threatened species of the world, many of which are in the public

consciousness: 'Darwin's finches' of the Galápagos Islands; Komodo dragons of Indonesia; the extinct Dodo of Réunion; moas of New Zealand; and elephant birds of Madagascar. Most recorded extinctions are of island species (Diamond, 2005), and many leading global conservation initiatives focus on islands as hotspots of biodiversity – e.g. six of the 25 hotspots defined by Myers *et al.* (2000) are archipelagos and four others are regions that include many important islands. Islands are interesting; islands are attractive; islands are valuable.

A fresh impetus

As research priorities change, researchers are again looking to island systems to gain fundamental insights – about how species arise, how they interact, and how they are threatened by a changing world (Tables 1, S1). In 2007, the 40th anniversary of MacArthur and Wilson's (1967) Princeton Monograph provided the occasion for a gathering of prominent biologists to assess the continuing impact of ETIB, and to examine how it has been extended and modified. That workshop, and the ensuing edited volume (Losos & Ricklefs, 2009), effectively brought to a close some older debates in island biogeography, including the 'single large or several small' (SLOSS) debate concerning the design of nature reserves (Laurance, 2009), and turned towards new horizons. Further momentum comes from new taxonomic, ecological, and molecular data (coupled with recent advances in analysing such data), and from new analytical approaches that allow stronger inference from island data (e.g. Bunnefeld & Phillimore, 2012). New syntheses in island biogeography are developing under a standard of multidisciplinarity and increasingly recognize the changing nature of the 'stage' on which life is played out (e.g. Whittaker *et al.*, 2008; Gravel *et al.*, 2011; Rosindell & Harmon, 2013; Fernández-Palacios *et al.*, this issue). A range of current developments in ecology and evolutionary biology can also be integrated into island-based research, making this an opportune moment to help frame the future of island biogeography.

This special issue of *Global Ecology and Biogeography* originated in a symposium at the British Ecological Society–INTECOL 2013 meeting in London in August, 2013, which marked the centenary of the death of the great island biogeographer, Alfred Russel Wallace, and the 50th anniversary of the initial appearance of the equilibrium theory of island biogeography in the journal *Evolution* (MacArthur & Wilson, 1963). The purpose of this special issue is not to look back at the influence of the ETIB, but instead to build on the current excitement in the literature (e.g. Fernández-Palacios *et al.*, 2015) and in recent conferences and highlight research directions being pioneered by a new generation of island biogeographers.

Although island research has recently contributed strongly to our understanding of species and lineage diversification (including ecological speciation and adaptive radiation; Box 1; e.g. Givnish, 1997; Schluter, 2000; Warren *et al.*, 2015), this special issue has more of an ecological flavour, though by no means exclusively so. It highlights new insights into island biogeography theory, particularly in terms of the geological "life-cycles" of islands (also termed ontogeny; Box 1) – that were partially acknowledge by Darwin (1842) and Wilson (1963), changes in archipelago geography caused by sea-level fluctuations, species addition (both colonization and *in situ* speciation), species' interactions, extinction, and area effects. The papers in this special issue focus strongly on processes not typically associated with the classical ETIB, particularly the roles of species' interactions, community assembly, environmental change, and evolution, in shaping island and island-like communities (though most of these were discussed to some extent by MacArthur and Wilson, 1967). These

processes include seed-dispersal and pollination networks at large spatial scales, as well as the influence of predation, mutualism and competition in structuring island communities. You will also find new perspectives on marine environments and on community assembly over ecological and evolutionary time. These topics inform our understanding of how global change will affect ecological communities, providing guidance for conservation and management. Finally, this issue covers niche (Box 1) evolution in relation to ecological opportunity and its influence on geographic distribution, and how the dynamics of island formation and demise, combined with changing sea levels and climates, influence the composition of island biotas. In the remainder of this opening contribution to the special issue, we highlight key areas of current research in island biogeography, locating the other papers within this wider context, and look ahead to further developments in the coming decade.

Advances and insights from island biogeography

Recent research on island systems has shifted towards broader themes in ecology and evolution that are considered global priorities for future work (Sutherland *et al.*, 2013). Among these themes is community assembly, for which islands can provide community-level entities with clear boundaries. The underlying processes are both local (e.g. physical conditions, resource limitation, competition) and regional (e.g. colonization, evolutionary diversification). The many islands of the world provide discrete 'natural experiments' replicated with respect to varying age, area, altitude, latitude, remoteness and local ecological conditions. The low number of species relative to mainland systems provides a level of simplicity that helps in understanding how species' interactions shape communities. Moreover, the 'disharmony' of many island biotas (i.e., the absence of entire groups of species that would be found in continental settings; Whittaker & Fernández-Palacios, 2007; Box 1) can be likened to manipulative experiments at a scale beyond the reach of researchers.

Species' interactions

Islands have figured prominently in research on how species interact. Early studies emphasized competition, as exemplified by the work of Diamond (1975) and others on 'assembly rules' governing how species' interactions influence community organization; more recent research has considered the roles of predators, pathogens and mutualists, including pollinators (e.g. Terborgh, 2001, Ricklefs & Bermingham, 2007). Network analysis, developed over the last two decades, is helping ecologists to understand species' interactions, particularly with respect to the organization of mutualistic networks involving pollinators and seed-dispersers (Bascompte & Jordano, 2007). Island pollination and seed-dispersal networks differ from those on the mainland (Traveset *et al.*, this issue) because of dispersal-driven biases in the types of species that can colonize islands (disharmony). Island networks are often simpler than mainland ones in having fewer species (e.g. González-Castro *et al.*, 2012; Traveset *et al.*, this issue), but they can be more complex owing to domination by generalist species (e.g. Olesen *et al.*, 2002; but see Olesen & Jordano, 2002).

Current research on interaction networks is taking a more macroecological/spatial perspective, including recent advances in evaluating large-scale geographical patterns of network properties (e.g. González-Castro *et al.*, 2012; Trøjelsgaard & Olesen, 2013). Traveset *et al.* (this issue) provide one of the first global comparisons of island and mainland pollination networks. They found that oceanic island (Box1) networks present higher niche

overlap among fewer species and links than mainland areas, and that, contrary to their expectations, pollinator/plant ratios, connectance, nestedness and modularity were similar in ecological communities on oceanic islands and mainlands (Box 1). In contrast, Nogales *et al.* (this issue) evaluated the modularity and nestedness patterns between two distant archipelagos (Canaries and Galápagos), finding very different patterns: the Canaries support highly nested networks and the Galápagos, modular ones.

The biodiversity of nearby source areas, combined with abiotic and biotic filters, can influence the diversity and character of island biotas (see Santos *et al.*, this issue). Extensive analyses of *Anolis* lizards in the Caribbean (Losos, 2011) and Darwin's finches (Aves: Geospizini) of the Galápagos Archipelago (Grant & Grant, 2008) have shown how communities can be shaped by competition and predation (e.g. Schoener, 1975; Spiller & Schoener, 1988). These studies provide clear examples of how the behaviour, habitat distribution, and phenotypes of populations can change in response to species' interactions (Grant & Grant, 2006; 2010) – in some cases causing evolutionary change observable over decades (e.g. Losos *et al.*, 2004; Grant & Grant, 2014). More recently, new models have arisen that describe the effects of trophic interactions in insular dynamics (e.g. Holt, 2009; Gravel *et al.*, 2011). Following these recent models, Cirtwill & Stouffer (this issue) evaluated effects of trophic relationships on immigration and extinction probabilities, finding that the inclusion of bottom-up effects (e.g. resource availability) improves ETIB predictions. Santos *et al.* (this issue) made a first attempt to understand global patterns of functional diversity and assembly of island faunas in their analysis of parasitoid faunas (Box 1). They concluded that the main determinant of parasitoid community assembly may be the structure of host communities. However, lack of information on host species distributions and host–parasitoid relationships prevents testing this hypothesis and emphasizes how much information we are still missing.

Species' interactions are often considered to drive Wilson's (1959, 1961) 'taxon cycle' (Box 1), in which competitively superior new colonists progressively exclude older colonists. Patterns consistent with taxon cycles have been described through phylogeographic analyses in several systems (e.g. Ricklefs & Bermingham, 2002; Economo & Sarnat, 2012; Jønsson *et al.*, 2014), but the underlying processes are poorly understood, particularly concerning the initiation of new expansion phases. Coevolutionary shifts in the balance between predators and their prey, or between pathogens and their hosts, might be involved (Ricklefs & Bermingham, 2002; Ricklefs, 2011). Regardless of the cause, species in expansion phases appear to colonize islands with little hindrance, suggesting that niche space on these islands is not filled. Many invasive species behave similarly (e.g. Sax *et al.*, 2002). Moreover, although taxon cycles have been documented primarily in island systems, they undoubtedly occur within continental areas (Glazier, 1980; Erwin, 1985) and apply at all geographic scales (Ricklefs, 2011). Indeed, the coevolutionary dynamics postulated to drive taxon cycles might produce intrinsic dynamics in ecological systems generally, which could influence patterns of distribution, abundance and even species production (Ricklefs, 2015). Finally, the ability of "expanding" species to invade new ecosystems, including "reverse" colonization from fairly small oceanic and continental islands to continents (Bellemain & Ricklefs, 2008; Patiño *et al.*, 2015), challenges the idea that continental communities are filled with species (but see Ricklefs, 2012; Harmon & Harrison, 2015; Rabosky & Hurlbert, 2015).

Area

Understanding the relationship between area and biological diversity has long been a major research focus in biogeography and ecology (e.g. MacArthur & Wilson, 1967; Rosenzweig,

1995) and was recently the focus of a 'virtual issue' of the *Journal of Biogeography* (see Whittaker & Triantis, 2012). In examining species–area relationships, Triantis *et al.* (2012; also see Gray *et al.*, 2004) drew attention to the fundamental distinction between species accumulation curves ('SACs' – the increase in species richness as a sampling property of progressively larger areas within regions) and island species–area relationships ('ISARs' – counts of species on different isolated islands). Their comprehensive meta-analysis of over 600 ISARs on true islands has now been added to by Matthews *et al.* (this issue), who used over 800 datasets from both habitat islands and true islands (Box 1) to evaluate how the slope (z) and intercept (c) of ISARs vary between island types. The slopes of the ISARs tended to be steeper on true islands, and oceanic islands had smaller intercepts than habitat islands within continental regions.

The dependence of extinction rate on island area (e.g. Ricklefs & Bermingham, 2007), in conjunction with the 'target effect' of larger islands being more likely to be colonised (Box 1; MacArthur, 1972), produces the familiar ISAR, reflecting the influence of island area on the dynamics of species gain and loss. Larger areas typically include more habitat types and support larger populations, promoting *in situ* speciation as well as reducing extinction rates. Losos and Schluter (2000) showed that the ISAR slope for Caribbean *Anolis* lizards increases above a critical island size that is apparently required for allopatric speciation within islands (Box 1). Building on that result, Algar and Mahler (this issue) found that the rate of climatic niche evolution in *Anolis* increases with island area, because of response to climatic opportunity, potentially contributing to adaptive diversification on larger islands. Consistent with a driving force on islands of response to opportunity, Steinbauer *et al.* (this issue) found high levels of climatic niche lability, rather than climatic niche conservatism or competitive displacement, within radiating plant clades in the Canary Islands.

Given those recent advances, it is not surprising that area affects not only species numbers, but also ecological interactions between island species (e.g. Holt, 2009; Gravel *et al.*, 2011; Roslin *et al.*, 2014). For islands in the Bahamas, Schoener *et al.* (this issue) found that competition and predation exhibited their largest effect sizes on intermediate-sized islands. They suggest that the harsher abiotic conditions, larger marine subsidies, lower spatial heterogeneity and greater stochastic effects typical of smaller islands shifted communities towards having fewer top predators compared to larger islands. In contrast, ant–plant mutualism decreased with increasing island area, while plant–pollinator mutualism showed the opposite trend.

The shifting stage

The recent history of island biogeographic investigation can be characterized as moving from a concept of islands as neutral, static and interchangeable landing pads for species (e.g. MacArthur & Wilson, 1963, 1967) to one in which their physical characteristics are critically important (e.g. Kalmar & Currie, 2006), and finally to a view of islands changing through time (e.g. Whittaker *et al.*, 2008; Rijsdijk *et al.*, 2014; Weigelt *et* al., 2016, Fernández-Palacios *et al.*, this issue). These considerations are in accordance with the general paradigm that Earth is a dynamic planet, where changes can even occur in short time spams. The 'General Dynamic Model' of oceanic island biogeography (GDM; Box 1; Whittaker *et al.*, 2008; see review by Borregaard *et al.*, in press a) emphasizes the importance of island ontogeny and geological dynamics for biological processes on islands, including colonization, speciation and extinction. The GDM has been evaluated empirically, receiving considerable support (e.g. Whittaker *et al.*, 2008; Borges & Hortal, 2009; Bunnefeld & Phillimore, 2012; Steinbauer *et al.*, 2013; Valente *et al.*, 2014). This model provides a good example of how island theory

is linked to other research areas. It implies that, early in island ontogeny, the main process acting is immigration, coupled with within-island and within-archipelago metapopulation and metacommunity dynamics. At a later stage (called the immaturity stage), the dynamic nature of island landscapes fosters the ascendance of evolutionary processes, at least on larger islands. Finally, as the island reaches its maturity and starts to submerge (due to erosion, downcutting, and subsidence), extinction increases and becomes the main driver of species richness and island community dynamics.

The GDM, as originally formulated (Whittaker *et al.*, 2008), was primarily applied to oceanic hotspot islands (Box 1). It has now been extended to include subduction-based arc islands and continental fragment islands (Box 1; Borregaard *et al.*, this issue; see also Heaney *et al.*, 2013). Borregaard *et al*. (this issue) also formalized the logic of the GDM, expressing the causal relationships as a directed graph model, which they used to evaluate the generalized diagram of 'key rates and properties' of Whittaker *et al*. (2008). This latest version of the GDM modifies the colonization and extinction curves and exposes a larger gap between potential species richness ('carrying capacity') and actual species richness throughout an island's life cycle.

The GDM does not include recent dramatic variations in climate and sea-level changes associated with Pleistocene glacial cycles (Ali & Aitchison, 2014; Rijsdijk *et al.*, 2014). To address these factors, Fernández-Palacios *et al.* (this issue) have produced a model of archipelagic island biogeography that combines the interconnected effects of sea-level changes, island area and isolation on immigration and extinction rates and, consequently, on species richness (see also Weigelt *et al.,* 2016). Furthermore, based on their model they enunciated testable predictions, regarding, for instance, species' genetic structure and extinction likelihood, which should enhance in the near future the study of the impact of sea level changes on the contemporary biotas of oceanic islands. Rominger *et al.* (this issue) have also incorporated archipelagic dynamics in their study of community assembly on the Hawaiian Islands. Hotspot archipelagos such as the Hawaiian Islands provide a time series over which one can investigate the evolutionary development of island biotas. Using extensive genetic and molecular phylogenetic information, Rominger *et al.* examined the development of ecological communities over the time series of the archipelago, where the major subaerial islands range from <0.5 Ma (Hawaii) to more than 5 Ma (Kauai), and new soils continue to form from recent lava flows on the youngest island, Hawaii. They found that ecological communities are initially driven by immigration, but that this shifts to *in situ* diversification after about 1 million years, resulting in changes in interaction network structure and ecological specialization (increase in modularity and decrease in nestedness) with increasing dominance of evolutionary change over time.

Human influences and biological invasions

Patterns of diversity and community organization on islands have, in many instances, been affected by human activities. The impacts of humans, and their commensals, on island biotas started in pre-historic times, as reflected by numerous extinctions apparent in the fossil record (Olson, 1990; Whittaker & Fernández-Palacios, 2007; Duncan *et al.*, 2013). Habitat conversion is one of the main threats to island species (e.g. Caujapé-Castells *et al.*, 2010; Triantis *et al.*, 2010), together with alien (Box 1) competitors, herbivores, predators and pathogens (e.g. Sax *et al.*, 2002; Reaser *et al.*, 2007; Caujapé-Castells *et al.*, 2010). Extinctions also affect functional diversity (Boyer *et al.*, 2014), which can influence ecosystem functioning. In some cases, introduced predators and herbivores have dramatically impacted local populations, sometimes shifting the entire ecological character

of an island – e.g. goats (Coblentz, 1978) and brown tree snakes (Savidge, 1987). In some archipelagos (e.g. Galápagos and Hawaii), the number of alien plant species surpasses that of natives, although it remains unclear how disruptive alien species are for interaction networks (e.g. Olesen *et al.*, 2002; Padrón *et al.*, 2009; Heleno *et al.*, 2013; Nogales *et al.*, this issue; but see Traveset & Richardson, 2006; Traveset *et al.*, 2013).

The native biotas of oceanic islands have developed through historic colonizations. What have changed with human transport and deliberate introductions are the rate of accumulation of new species and the appearance of species with limited dispersal ability that would not reach many islands without human assistance. Introduced species (and also historic extinctions) provide opportunities to observe how new species fit into established communities (Sax *et al.*, 2002; Nogales *et al.*, this issue), and how their introduction alters community relationships. Blackburn *et al.* (this issue) used structural equation modelling to explore these questions, and found that both native and alien plants and birds have strikingly similar (positive) ISARs. They found that alien species richness was strongly positively related to both native species richness and human population size, interpreting human population size as a measure of propagule pressure, and native species richness as a proxy for the island environment. These results suggest that native and alien species richness respond similarly to the same factors on islands, while biotic resistance (*sensu* Elton, 1958) is not a major influence.

The future of island biogeography

Island biogeography is currently enjoying a renaissance (Fernández-Palacios et al., 2015). Much of the knowledge gathered through the last decades from different research areas is being synthesized in new theories and models – two of them being included in this special issue (Borregaard *et al.,* in press b; Fernández-Palacios *et al.*, in press; Table 1), while existing ones are being tested and updated with new and more powerful analytical tools and new molecular, ecological and distributional data. Because islands' circumscribed geography and discrete nature allow the study of the geography of processes that are, in fact, occurring everywhere – including within large continental regions and ocean basins (examples in Table 1) – we believe this integration of knowledge arising from island studies will surely have an impact in terms of understanding other systems.

Despite this surge of research activity, some avenues for future research remain relatively unexplored. Heaney *et al.* (2013) and Warren *et al.* (2015) proposed a number of research questions that involve islands as key elements for understanding the ecological and evolutionary processes shaping communities in general. More particularly, they refer to questions related to (i) community assembly – the importance of arrival history (or priority effects; Box 1) for community assembly, changes in species' abundance that might occur after colonization, the influence of existing species on the establishment of newly arrived species, and influence of island area and isolation on community assembly, equilibrium, and evolution; (ii) ecosystem functioning – particularly the contribution of *in situ* evolution to changes in rates of energy flux and nutrient cycling; and (iii) speciation and diversification – the role of gene flow in speciation, and the more rapid diversification of some lineages in comparison with others. These priorities reinforce the need to incorporate non-equilibrium dynamics and different modes of speciation in future island models. Here we complement these prospects and propose some questions that we feel should be pursued. We first discuss broad research directions that are not island-specific, but to which islands might

contribute important insights. We then briefly cover additional questions that may not be so directly transferable to continental areas.

Islands, particularly oceanic islands that have long been isolated from the mainland, have their own peculiarities (e.g. species with unusual adaptations as in the cases of woodpecker finches and blood-sucking finches on the Galápagos Islands, dragon's blood trees on Socotra and Macaronesia, pollinating reptiles on many islands). To transfer knowledge appropriately from islands to broader contexts requires understanding both the similarities that promote transferability and the differences that limit it. For example, adaptive radiation, a process widely studied on islands (e.g. Givnish *et al.*, 2009; Losos, 2011; Steinbauer *et al.*, this issue), occurs differently on islands and continental areas. In island systems, speciation tends to occur in isolation within lineages (e.g. Pinto *et al.*, 2008), while on continents it is common for radiations to involve evolution in many lineages, interacting through antagonistic or mutualistic relationships. Island–mainland (or species pool) comparisons seem to be a logical way to proceed, but few studies have taken this approach (but see Santos *et al.*, 2011a, 2011b; Patiño *et al.,* 2015; Traveset *et al.*, this issue). Some that have done so have questioned old assumptions about islands – for example: island communities do not always have lower diversity than mainland communities (e.g. Algar & Losos, 2011; Patiño *et al.*, 2015); the island rule does not hold true for many taxa (Box 1; e.g. Meiri *et al.*, 2008; Itescu *et al.*, 2014); island systems are not necessarily dominated by species with high dispersal capacities (e.g. Vargas *et al.*, 2012; Heleno & Vargas, 2015). With more data and analytical approaches available than ever before, more effort should be directed towards understanding the generality of patterns and processes that have been widely acknowledged as being predominant on islands, and that have long been used to separate island from mainland systems.

Community assembly on oceanic islands involves (i) the dispersal of species from an external species pool, following which the species are then (ii) subjected to abiotic and biotic filters that determine the island or within-island assemblage. These two steps also occur on continental islands, although they are less important as newly formed continental islands already possess a diverse biota. The species pool can be defined as the group of species that can potentially colonize a local site (Cornell & Harrison, 2014); the species pool is generally thought of as a static and independent (i.e. extrinsic) unit (Mittelbach & Schemske, 2015). The species pool concept has been widely used as a null model for identifying processes (e.g. environmental filtering, limiting similarity) that shape the taxonomic, phylogenetic or trait structure of communities (e.g. Carstensen *et al.*, 2013; Weigelt *et al.*, 2015; Santos *et al.*, this issue). Although this top-down framework has been widely applied (e.g. MacArthur & Wilson, 1963; Hubbell, 2001), it fails to incorporate the dynamic nature of the species pool, and the importance of dispersal, speciation and extinction for the maintenance of the species pool over time and space. Archipelagos can help us understand how local species assemblages and regional species pools are linked within continents, as each archipelago can be viewed as a regional pool that feeds, and is fed by, the dynamics occurring within and between its constituent islands (local assemblages; Grant & Grant, 2008). Species arising in allopatry might colonize other islands, achieving secondary sympatry and becoming part of the archipelagic species pool (islands feed the pool), eventually colonizing other islands within the archipelago (the pool feeds the islands).

The Earth is currently going through dramatic environmental changes (e.g. pollution, climate changes, land use change, biodiversity loss) that are affecting many of the planet's ecosystem support systems, and that can ultimately lead to species' extinctions and further deterioration of human societies. Islands are also subject to these impacts (e.g. Savidge,

1987; Sax *et al.*, 2002; Duncan *et al.,* 2013*;* Boyer & Jetz, 2014; Bellard *et al*., 2014) and can be useful tools for understanding the consequences of environmental change. First, as islands (or archipelagos) are discrete and geographically isolated, most of their populations cannot easily escape these impacts. Second, as many islands are among the last territories to be colonized by humans, the impact of human activity has been occurring for a shorter period of time, which provides the opportunity to disentangle the effects of climate change on the extinction of local communities.

Biological invasions can fundamentally change the local biotic environment (e.g. van der Wal *et al.,* 2008). Islands have been particularly affected by invasions (Sax *et al.*, 2002), with many island faunas and floras now being dominated by introduced species (e.g. Azores, Hawaii). Islands offer great opportunities for research into biological invasions because of their well delimited boundaries and, in many cases, relatively brief periods of human occupation (Sax *et al.*, 2002) and knowledge of approximate human arrival dates. Further, as many islands are within archipelagos, they have been subject to similar evolutionary histories and ecological forces, providing replicated units with varying degrees of species' introductions. Sax and Gaines (2008) described four principal knowledge gaps in invasion research: (i) the need to further understand the role of propagule pressure, (ii) the dynamics of time-lags to extinction, (iii) the effects of alien species on native species' abundance, and (iv) the impact of land-use changes on native species diversity. To these, we add the important question of how invasive species affect ecosystem functioning: do they replace native species' functions, add functions not previously performed, or become redundant in terms of the ecosystem functions they provide?

Some questions that apply specifically to island systems also address research priorities for ecology more generally. Trait diversity and phylogenetic diversity have been widely used over the past decade as tools to ascertain the processes that shape community assembly, particularly in continental areas. Typically, ecologists assume that communities are shaped either by limiting similarity (resulting in coexistence of species that are overdispersed in ecological and trait space) or environmental filtering (causing clustered patterns), with contradictions when traits are not phylogenetically conserved (Pausas & Verdú, 2010). So far, few studies on island systems have analysed community organization from this perspective (but see Cardillo & Meijaard, 2010; Santos *et al.*, this issue). Island systems, with their relative simplicity, could be used to combine such research with investigation of other processes potentially involved in community assembly, but which are more difficult to address in continental contexts (e.g. convergent evolution, adaptive radiation). Our knowledge of the biogeography of trait and phylogenetic diversity is still limited. For example, what is the relationship between trait and/or phylogenetic diversity and species richness on islands? Does this relationship differ from that found in mainland systems? How are trait and/or phylogenetic diversity related to island area and age?

One of ETIB's main predictions is that species on islands are continually being turned over through extinction and colonization, with species richness becoming stable through time (MacArthur & Wilson, 1967). Yet, few studies have addressed the dynamics of these processes (but see Valente *et al.*, 2015). One prediction that should be evaluated is that islands have a mix of young and old species, which can now be assessed through phylogenetic reconstructions (Ricklefs & Bermingham, 2001, 2008; Cadena *et al.*, 2005; Valente *et al.*, 2014). However, this pattern could also arise in a non-saturated island, where no extinctions have occurred. Quantifying extinctions, particularly the timing of extinctions, is difficult in most island settings. One approach that could be more fully explored is fitting

species' age distributions to models that incorporate extinction, assuming time-homogeneous processes (Ricklefs, 2009).

Where species diversification occurs within islands, we would also like to understand how this process varies over the geological ontogeny of individual islands. According to the General Dynamic Model (Whittaker *et al.*, 2008; Borregaard *et al.*, this issue), speciation rate should be higher in relatively young islands, which provide opportunities for diversification due to empty ecological niche space, and when extinction rates may be relatively low. Although a few studies have looked into this question using modelling approaches (e.g. Rabosky & Glor, 2010; Valente *et al.*, 2014), empirical evaluation is largely lacking (see, however, Fritz *et al.*, 2012).

Concluding remarks

From the observations and patterns described by naturalists during the first European expeditions around the globe, to the studies by Darwin and Wallace, and to the development of the Equilibrium Theory of Island Biogeography (Box 1), islands have long influenced our understanding of ecological and evolutionary patterns and processes (Table 1, S1). This interest continues to the present, reinvigorated by new perspectives and analytical approaches to community ecology, evolutionary diversification and biogeographic distributions of species. This special issue of *Global Ecology and Biogeography* is a reflection of the continued relevance of island systems for understanding ecology and evolution more generally. We hope you agree that the papers in this special issue set a good collective example for continuing research on island systems.

Existing datasets from island systems are globally valuable and have provided important insights for ecology and evolution, largely because of the relative simplicity and possibility for independent replication offered by islands and archipelagos. However, although databases for island characteristics, and for species distributions and ecological requirements, traits, and phylogenetic relationships continue to grow (e.g. Cardillo & Meijaard, 2010; Weigelt *et al*., 2013, 2015; Whittaker *et al.*, 2014; Santos *et al*., this issue), many gaps need filling to realize the full potential of future research. Inventories of island floras and faunas, particularly of non-vertebrate groups, are far from complete (e.g. Hortal *et al*., 2007; Schipper *et al*., 2008; Santos *et al*., 2010), with many species still waiting to be described. Detailed information on the distribution of species within islands, which could be used for investigation of community assembly and, in some systems, adaptive radiation, is still limited in many cases. More information on functional traits and phylogenetic relationships may help us to interpret community assembly and structure in terms of ecological and evolutionary processes, including adaptive radiation. We advocate a continuing effort to build comprehensive island data for multiple taxa, to serve the wider scientific community in the coming decades.

The current excitement around islands reflects island biogeography's being a vibrant, active field of research. We hope this enthusiasm will continue and that the knowledge and theories developed from island systems will continue to produce insight into the natural world more generally.

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References

Algar, A.C. & J. B. Losos (2011) Evolutionary assembly of island faunas reverses the classic island–mainland richness difference in *Anolis* lizards. *Journal of Biogeography*, **38**, 1125–37.

Algar, A.C. & Mahler, D.L. (in press) Area, climate heterogeneity, and the response of climate niches to ecological opportunity in island radiations of *Anolis* lizards. *Global Ecology and Biogeography*.

Ali, J.R. & J.C. Aitchison (2014) Exploring the combined role of eustasy and oceanic island thermal subsidence in shaping biodiversity on the Galápagos. *Journal of Biogeography*, **41**, 1227–41.

Bascompte, J. & Jordano, P. (2007) Plant–animal mutualistic networks: the architecture of biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, **38**, 567–593.

Bellard, C., Leclerc, C. & Courchamp, F. (2014) Impact of sea level rise on the 10 insular biodiversity hotspots. *Global Ecology and Biogeography*, **23**, 203–212.

Bellemain, E. & Ricklefs, R.E. (2008) Are islands the end of the colonization road? *Trends in Ecology & Evolution*, **23**, 461–468.

Blackburn, T.M., Delean, S., Pyšek, P. & Cassey, P. (in press) On the island biogeography of aliens: a global analysis of the richness of plant and bird species on oceanic islands. *Global Ecology and Biogeography*.

Borges, P.A.V. & Hortal, J. (2009) Time, area and isolation: factors driving the diversification of Azorean arthropods. *Journal of Biogeography*, **36**, 178–191.

Borregaard, M. K., Amorim, I. R., Borges, P. A. V., Cabral, J. S., Fernández-Palacios, J. M., Field, R., Heaney, L. R., Kreft, H., Matthews, T. J., Olesen, J. M., Price, J., Rigal, F., Steinbauer, M. J., Triantis, K. A., Valente, L., Weigelt, P. & Whittaker, R. J. (in press a) Oceanic island biogeography through the lens of the general dynamic model: assessment and prospect. *Biological Reviews*.

Borregaard, M.K., Matthews, T.J. & Whittaker, R.J. (in press b) The general dynamic model: towards a unified theory of island biogeography? *Global Ecology and Biogeography*.

Boyer, A.G. & Jetz, W. (2014) Extinctions and the loss of ecological function in island bird communities. *Global Ecology and Biogeography*, **23**, 679–688.

Brown, J.H. (1971) Mammals on mountaintops: nonequilibrium insular biogeography. *The American Naturalist*, **105**, 467–478.

Brown, J.H. (1978) The theory of insular biogeography and the distribution of boreal birds and mammals. *Great Basin Naturalist Memoirs*, **2**, 209–277.

Brown, J. H. (1981) Two decades of Homage to Santa Rosalia: toward a general theory of diversity. *American Zoologist*, **21**, 877–888.

Brown, J.H. (2004) Toward a metabolic theory of ecology. *Ecology*, **85**, 1771–1789.

Bunnefeld, N. & Phillimore, A.B. (2012) Island, archipelago and taxon effects: mixed models as a means of dealing with the imperfect design of nature's experiments. *Ecography*, **35**, 15–22.

Cadena, C.D., Ricklefs, R.E., Jimenez, I. & Bermingham, E. (2005) Ecology – Is speciation driven by species diversity? *Nature*, **438**, E1–E2.

Cardillo, M. & Meijaard, E. (2010) Phylogeny and co-occurrence of mammal species on Southeast Asian islands. *Global Ecology and Biogeography*, **19**, 465–474.

Carstensen, D.W., Lessard, J.-P., Holt, B.G., Borregaard, M.K. & Rahbek, C. (2013) Introducing the biogeographic species pool. *Ecography*, **36**, 1310–1318.

Caujapé-Castells, J., Tye, A., Crawford, D.J., Santos-Guerra, A., Sakai, A., Beaver, K., Lobin, W.,

Vincent Florens, F.B., Moura, M., Jardim, R., Gómes, I. & Kueffer, C. (2010) Conservation of oceanic island floras: Present and future global challenges. *Perspectives in Plant Ecology, Evolution and Systematics*, **12**, 107–129.

Cirtwill, A.R. & Stouffer, D.B. (in press) Knowledge of predator–prey interactions improves predictions of immigration and extinction in island biogeography. *Global Ecology and Biogeography*.

Coblentz, B.E. (1978) The effects of feral goats (*Capra hircus*) on island ecosystems. *Biological Conservation*, **13**, 279–286.

Connor, E.F. & Simberloff, D. (1979) The assembly of species communities: chance or competition? *Ecology*, **60**, 1132–1140.

Cornell, H.V. & Harrison, S.P. (2014) What are species pools and when are they important? *Annual Review of Ecology, Evolution, and Systematics*, **45**, 45–67.

Darwin C.R. (1842). *The structure and distribution of coral reefs. Being the first part of the geology of the voyage of the Beagle, under the command of Capt. Fitzroy, R.N. during the years 1832 to 1836*. Smith Elder and Co., London.

Dawson, M.N. (in press) Island and island-like marine environments. *Global Ecology and Biogeography*.

Diamond, J.M. (1975) Assembly of species communities. *Ecology and evolution of communities* (ed. by M.L. Cody and J.M. Diamond), pp. 342–444. Harvard University Press, Cambridge, MA.

Diamond, J.M. (2005) *Collapse: how societies choose to fail or survive*. Allen Lane/Penguin, London.

Duncan, R.P., Boyer, A.G. & Blackburn, T.M. (2013) Magnitude and variation of prehistoric bird extinctions in the Pacific. *Proceedings of the National Academy of Sciences*, **110**, 6436–6441.

Economo, E.P. & Sarnat, E.M. (2012) Revisiting the ants of Melanesia and the taxon cycle: historical and human-mediated invasions of a tropical archipelago. *The American Naturalist*, **180**, E1–E6.

Elton, C.S. (1958) *The ecology of invasions by animals and plants*. Methuen, London.

Erwin, T.L. (1985) The taxon pulse: a general pattern of lineage radiation and extinction among carabid beetles. *Taxonomy, phylogeny, and zoogeography of beetles and ants: a volume dedicated to the memory of Philip Jackson Darlington, Jr., 1904–1983* (ed. by G.E. Ball), pp. 437–472. Dr W. Junk Publishers, Dordrecht.

Fernández-Palacios, J.-M., Kueffer, C. & Drake, D. (2015) A new golden era in island biogeography. *Frontiers of Biogeography*, **7**, 14–20.

Fernández-Palacios, J.M., Rijsdijk, K.F., Norder, S.J., Otto, R., de Nascimento, L., Fernández-Lugo, S., Tjørve, E. & Whittaker, R.J. (in press) Towards a glacial-sensitive model of island biogeography. *Global Ecology and Biogeography*.

Fritz, S.A., Jønsson, K.A., Fjeldså, J. & Rahbek, C. (2012) Diversification and biogeographic patterns in four island radiations of passerine birds. *Evolution*, **66**, 179–190.

Givnish, T.J. (1997) Adaptive radiation and molecular systematics: aims and conceptual issues. *Molecular evolution and adaptive radiation* (ed. by T.J. Givnish and K.J. Sytsma), pp. 1–54. Cambridge University Press, New York.

Givnish, T.J., Millam, K.C., Mast, A.R., Paterson, T.B., Theim, T.J., Hipp, A.L., Henss, J.M., Smith, J.F., Wood, K.R. & Sytsma, K.J. (2009) Origin, adaptive radiation and diversification of the Hawaiian lobeliads (Asterales: Campanulaceae). *Proceedings of the Royal Society B: Biological Sciences*, **276**, 407–416.

Glazier, D.S. (1980) Ecological shifts and the evolution of geographically restricted species of

North American *Peromyscus* (mice). *Journal of Biogeography*, **7**, 63–83.
González-Castro, A., Traveset, A. & Nogales, M. (2012) Seed dispersal interactions in the Mediterranean Region: contrasting patterns between islands and mainland. *Journal of Biogeography*, **39**, 1938–1947.
Gotelli, N.J. & Graves, G.R. (1996) *Null models in ecology*. Smithsonian Institution Press, Washington, D. C.
Grant, P.R. & Grant, B.R. (2006) Evolution of character displacement in Darwin's Finches. *Science*, **313**, 224–226.
Grant, P.R. & Grant, B.R. (2008) *How and why species multiply. The radiation of Darwin's Finches*. Princeton University Press, Princeton, N.J.
Grant, B.R. & Grant, P.R. (2010) Songs of Darwin's finches diverge when a new species enters the community. *Proceedings of the National Academy of Sciences*, **107**, 20156–20163.
Grant, P.R. & Grant, B.R. (2014) *40 years of evolution: Darwin's Finches on Daphne Major Island*. Princeton University Press, Princeton, N. J.
Gravel, D., Massol, F., Canard, E., Mouillot, D. & Mouquet, N. (2011) Trophic theory of island biogeography. *Ecology Letters*, **14**, 1010–1016.
Gray, J.S., Ugland, K.I. & Lambshead, J. (2004) On species accumulation and species–area curves. *Global Ecology and Biogeography*, **13**, 567–568.
Harmon, L.J. & Harrison, S. (2015) Species diversity is dynamic and unbounded at local and continental scales. *The American Naturalist*, **185**, 584–593.
Heaney, L.R., Balete, D.S. & Rickart, E.A. (2013) Models of oceanic island biogeography: changing perspectives on biodiversity dynamics in archipelagoes. *Frontiers of Biogeography*, **5**, 249–257.
Heleno, R. & Vargas, P. (2015) How do islands become green? *Global Ecology and Biogeography*, **24**, 518–526.
Heleno, R.H., Olesen, J.M., Nogales, M., Vargas, P. & Traveset, A. (2013) Seed dispersal networks in the Galápagos and the consequences of alien plant invasions. *Proceedings of the Royal Society B: Biological Sciences*, **280**
Holt, R.D. (2009) Toward a trophic island biogeography. Reflections on the interface of island biogeography and food web ecology. *The theory of island biogeography revisited* (ed. by J.B. Losos and R.E. Ricklefs), pp. 143–185. Princeton University Press, Princeton, NJ.
Hortal, J., Lobo, J.M. & Jiménez-Valverde, A. (2007) Limitations of biodiversity databases: case study on seed-plant diversity in Tenerife, Canary Islands. *Conservation Biology*, **21**, 853–863.
Hubbell, S.P. (2001) *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton.
Itescu, Y., Karraker, N.E., Raia, P., Pritchard, P.C.H. & Meiri, S. (2014) Is the island rule general? Turtles disagree. *Global Ecology and Biogeography*, **23**, 689–700.
Jønsson, K.A., Irestedt, M., Christidis, L., Clegg, S.M., Holt, B.G. & Fjeldså, J. (2014) Evidence of taxon cycles in an Indo-Pacific passerine bird radiation (Aves: Pachycephala). *Proceedings of the Royal Society B: Biological Sciences*, **281**
Kalmar, A. & Currie, D.J. (2006) A global model of island biogeography. *Global Ecology & Biogeography*, **15**, 72–81.
Laurance, W.F. (2009) Beyond island biogeography theory. Understanding habitat fragmentation in the real world. *The Theory of Island Biogeography Revisited* (ed. by J.B. Losos and R.E. Ricklefs), pp. 214–236. Princeton University Press, Princeton, NJ.
Leigh Jr., E.G. (2007) Neutral theory: a historical perspective. *Journal of Evolutionary Biology*, **20**, 2075–2091.

Losos, J.B. (2004) Adaptation and speciation in Greater Antillean anoles. *Adaptive Speciation* (ed. by U. Dieckmann, M. Doebeli, J.A.J. Metz and D. Tautz), pp. 335–343. Cambridge University Press, Cambridge, U.K.

Losos, J. (2011) *Lizards in an evolutionary tree. Ecology and adaptive radiation of Anoles*. University of California Press, Berkeley.

Losos, J.B. & Schluter, D. (2000) Analysis of an evolutionary species–area relationship. *Nature*, **408**, 847–850.

Losos, J.B. & Ricklefs, R.E. (2009) *The theory of island biogeography revisited*. Princeton University Press.

MacArthur, R.H. (1972) *Geographical ecology. Patterns in the distribution of species*. Harper and Row, New York.

MacArthur, R.H. & Wilson, E.O. (1963) An equilibrium theory of insular zoogeography. *Evolution*, **17**, 373–387.

MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey.

March, F. & Bass, D. (1995) Application of island biogeography theory to temporary pools. *Journal of Freshwater Ecology*, **10**, 83–85.

Matthews, T.J., Guilhaumon, F., Triantis, K.A., Borregaard, M.K. & Whittaker, R.J. (in press) On the form of species–area relationships in habitat islands and true islands. *Global Ecology and Biogeography*.

Meiri, S., Cooper, N. & Purvis, A. (2008) The island rule: made to be broken? *Proceedings of the Royal Society B: Biological Sciences*, **275**, 141–148.

Mittelbach, G.G. & Schemske, D.W. (2015) Ecological and evolutionary perspectives on community assembly. *Trends in Ecology & Evolution*, **30**, 241–247.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonserca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.

Nogales, M., Heleno, R., Rumeu, B., González-Castro, A., Traveset, A., Vargas, P. & Olesen, J.M. (in press) Seed-dispersal networks on the Canaries and the Galápagos archipelagos: interaction modules as biogeographical entities. *Global Ecology and Biogeography*.

Olesen, J.M. & Jordano, P. (2002) Geographic patterns in plant–pollinator mutualistic networks. *Ecology*, **83**, 2416–2424.

Olesen, J.M., Eskildsen, L.I. & Venkatasamy, S. (2002) Invasion of pollination networks on oceanic islands: importance of invader complexes and endemic super generalists. *Diversity and Distributions*, **8**, 181–192.

Olson, S.L. (1990) The prehistoric impact of man on biogeographical patterns of insular birds. *Atti dei Covegni Lincei*, **85**, 45–51.

Padrón, B., Traveset, A., Biedenweg, T., Díaz, D., Nogales, M. & Olesen, J.M. (2009) Impact of alien plant invaders on pollination networks in two archipelagos. *PlosOne*, **4**, e627.

Patiño, J., Carine, M.A., Mardulyn, P., Devos, N., Mateo, R.G., González-Mancebo, J.M., Shaw, A.J. & Vanderpoorten, A. (2015) Approximate Bayesian computation reveals the crucial role of oceanic islands for the assembly of continental biodiversity. *Systematic Biology*, **64**, 579–589.

Pausas, J.G. & Verdú, M. (2010) The jungle of methods for evaluating phenotypic and phylogenetic structure of communities. *BioScience*, **60**, 614–625.

Pimm, S.L. (1991) *The balance of nature?: Ecological issues in the conservation of species and communities.* University of Chicago Press, Chicago.

Pinto, G., Mahler, D.L., Harmon, L.J. & Losos, J.B. (2008) Testing the island effect in adaptive radiation: rates and patterns of morphological diversification in Caribbean and mainland

Anolis lizards. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 2749–2757.
Preston, F.W. (1962a) The canonical distribution of commonness and rarity: part I. *Ecology*, **43**, 185–215.
Preston, F.W. (1962b) The canonical distribution of commonness and rarity: part II. *Ecology*, **43**, 410–432.
Rabosky, D.L. & Glor, R.E. (2010) Equilibrium speciation dynamics in a model adaptive radiation of island lizards. Proceedings of the National Academy of Sciences, 107, 22178–22183.
Rabosky, D.L. & Hurlbert, A.H. (2015) Species richness at continental scales is dominated by ecological limits. *The American Naturalist*, **185**, 572–583.
Reaser, J.K., Meyerson, L.A., Cronk, Q., De Poorter, M., Eldrege, L.G., Green, E., Kairo, M., Latasi, P., Mack, R.N., Mauremootoo, J., O'Dowd, D., Orapa, W., Sasatroutomo, S., Suanders, A., Shine, C., Thrainsoon, S. & Vaiutu, L. (2007) Ecological and socioeconomic impacts of invasive alien species in island ecosystems. *Environmental Conservation*, **34**, 98–111.
Ricklefs, R.E. (2006) The unified neutral theory of biodiversity: do the numbers add up? *Ecology*, **87**, 1424–1431.
Ricklefs, R.E. (2009) Dynamics of colonization and extinction on islands. Insights from Lesser Antillean birds. *The Theory of Island Biogeography Revisited* (ed. by J.B. Losos and R.E. Ricklefs), pp. 388–414. Princeton University Press, Princeton, N. J.
Ricklefs, R.E. (2011) A biogeographical perspective on ecological systems: some personal reflections. *Journal of Biogeography*, **38**, 2045–2056.
Ricklefs, R.E. (2012) Species richness and morphological diversity of passerine birds. *Proceedings of the National Academy of Sciences*, **109**, 14482–14487.
Ricklefs, R.E. (2015) Intrinsic dynamics of the regional community. *Ecology Letters*, **18**, 497–503.
Ricklefs, R.E. & Bermingham, E. (2001) Nonequilibrium Diversity Dynamics of the Lesser Antillean Avifauna. *Science*, **294**, 1522–1524.
Ricklefs, R.E. & Bermingham, E. (2002) The concept of the taxon cycle in biogeography. *Global Ecology and Biogeography*, **11**, 353–361.
Ricklefs, R.E. & Bermingham, E. (2007) The causes of evolutionary radiations in archipelagoes: passerine birds in the Lesser Antilles. *The American Naturalist*, **169**, 285–297.
Ricklefs, R. & Bermingham, E. (2008) The West Indies as a laboratory of biogeography and evolution. *Philosophical Transactions of the Royal Society of London. Series B – Biological Sciences*, **363**, 2393–2413.
Rijsdijk, K. F., Hengl, T., Norder, S. J., Otto, R., Emerson, B. C., Ávila, S. P., López, H., Van Loon, E. E., Tjørve, E. & Fernández-Palacios, J. M. (2014) Quantifying surface-area changes of volcanic islands driven by Pleistocene sea-level cycles: biogeographical implications for the Macaronesian archipelagos. *Journal of Biogeography*, **41**, 1242–54.
Rominger, A.J., Goodman, K.R., Lim, J.Y., Armstrong, E.E., Becking, L.E., Bennett, G.M., Brewer, M.S., Cotoras, D.D., Ewing, C.P., Harte, J., Martinez, N.D., O'Grady, P.M., Percy, D.M., Price, D.K., Roderick, G.K., Shaw, K.L., Valdovinos, F.S., Gruner, D.S. & Gillespie, R.G. (in press) Community assembly on isolated islands: macroecology meets evolution. *Global Ecology and Biogeography*.
Rosenzweig, M.L. (1975) On continental steady states of species diversity. *Ecology and evolution of communities* (ed. by M.L. Cody and J.M. Diamond), pp. 121–140. Harvard University Press, Cambridge, Massachusetts.
Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press,

Cambridge, UK.
Rosindell, J. & Phillimore, A.B. (2011) A unified model of island biogeography sheds light on the zone of radiation. *Ecology Letters*, **14**, 552–560.
Rosindell, J. & Harmon, L.J. (2013) A unified model of species immigration, extinction and abundance on islands. *Journal of Biogeography*, **40**, 1107–1118.
Roslin, T., Várkonyi, G., Koponen, M., Vikberg, V. & Nieminen, M. (2014) Species–area relationships across four trophic levels – decreasing island size truncates food chains. *Ecography*, **37**, 443–453.
Santos, A.M.C., Jones, O.R., Quicke, D.L.J. & Hortal, J. (2010) Assessing the reliability of biodiversity databases: identifying evenly inventoried island parasitoid faunas (Hymenoptera: Ichneumonoidea) worldwide. *Insect Conservation and Diversity*, **3**, 72–82.
Santos, A.M.C., Fontaine, C., Quicke, D.L.J., Borges, P.A.V. & Hortal, J. (2011a) Are island and mainland biotas different? Richness and level of generalism in parasitoids of a microlepidopteran in Macaronesia. *Oikos*, **120**, 1256–1262.
Santos, A.M.C., Quicke, D.L.J., Borges, P.A.V. & Hortal, J. (2011b) Species pool structure determines the degree of generalism of island paraistoid faunas. *Journal of Biogeography*, **38**, 1657–1667.
Santos, A.M.C., Cianciaruso, M.V. & De Marco, P. (in press) Global patterns of functional diversity and assemblage structure of island parasitoid faunas. *Global Ecology and Biogeography* .
Savidge, J.A. (1987) Extinction of an island forest avifauna by an introduced snake. *Ecology*, **68**, 660–668.
Sax, D.F. & Gaines, S.D. (2008) Species invasions and extinction: The future of native biodiversity on islands. *Proceedings of the National Academy of Sciences*, **105**, 11490–11497.
Sax, D.F., Gaines, S.D. & Brown, J.H. (2002) Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. *The American Naturalist*, **160**, 766–783.
Schipper, J., Chanson, J.S., Chiozza, F., Cox, N.A., Hoffmann, M., Katariya, V., Lamoreux, J., Rodrigues, A.S.L., Stuart, S.N., Temple, H.J., Baillie, J., Boitani, L., Lacher, J., T.E., Mittermeier, R.A., Smith, A.T., Absolon, D., Aguiar, J.M., Amori, G., Bakkour, N., Baldi, R., Berridge, R.J., Bielby, J., Black, P.A., Blanc, J.J., Brooks, T.M., Burton, J.A., Butynski, T.M., Catullo, G., Chapman, R., Cokeliss, Z., Collen, B., Conroy, J., Cooke, J.G., da Fonseca, G.A.B., Derocher, A.E., Dublin, H.T., Duckworth, J.W., Emmons, L., Emslie, R.H., Festa-Bianchet, M., Foster, M., Foster, S., Garshelis, D.L., Gates, C., Gimenez-Dixon, M., Gonzalez, S., Gonzalez-Maya, J.F., Good, T.C., Hammerson, G., Hammond, P.S., Happold, D., Happold, M., Hare, J., Harris, R.B., Hawkins, C.E., Haywood, M., Heaney, L.R., Hedges, S., Helgen, K.M., Hilton-Taylor, C., Hussain, S.A., Ishii, N., Jefferson, T.A., Jenkins, R.K.B., Johnston, C.H., Keith, M., Kingdon, J., Knox, D.H., Kovacs, K.M., Langhammer, P., Leus, K., Lewison, R., Lichtenstein, G., Lowry, L.F., Macavoy, Z., Mace, G.M., Mallon, D.P., Masi, M., McKnight, M.W., Medellin, R.A., Medici, P., Mills, G., Moehlman, P.D., Molur, S., Mora, A., Nowell, K., Oates, J.F., Olech, W., Oliver, W.R.L., Oprea, M., Patterson, B.D., Perrin, W.F., Polidoro, B.A., Pollock, C., Powel, A., Protas, Y., Racey, P., Ragle, J., Ramani, P., Rathbun, G., Reeves, R.R., Reilly, S.B., Reynolds, I., J.E., Rondinini, C., Rosell-Ambal, R.G., Rulli, M., Rylands, A.B., Savini, M., Schank, C.J., Sechrest, W., Self-Sullivan, C., Shoemaker, A., Sillero-Zubiri, C., De Silva, N., Smith, D.E., Srinivasulu, C., Stephenson, P.J., van Strien, N., Talukdar, B.K., Taylor, B.L., Timmins, R., Tirira, D.G., Tognelli, M.F., Tsytsulina, K., Veiga, L.M., Vié, J.-C., Williamson, E.A., Wyatt, S.A., Xie, Y. & Young, B.E. (2008) The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science*, **322**, 225–230.

Schluter, D. (2000) *The ecology of adaptive radiation*. Oxford University Press, Oxford.
Schoener, T.W. (1975) Presence and absence of habitat shift in some widespread lizard species. *Ecological Monographs*, **45**, 233–258.
Schoener, T.W., Spiller, D.A. & Piovia-Scott, J. (in press) Variation in ecological interaction strength with island area: theory and data from the Bahamian archipelago. *Global Ecology and Biogeography*.
Simberloff, D. & Collins, M.D. (2009) Birds of the Solomon Islands. The domain of the dynamic equilibrium theory and assembly rules, with comments on the taxon cycle. *The Theory of Island Biogeography Revisited* (ed. by J.B. Losos and R.E. Ricklefs), pp. 237–263. Princeton University Press, Princeton, NJ.
Spiller, D.A. & Schoener, T.W. (1988) An experimental study of the effect of lizards on web-spider communities. *Ecological Monographs*, **58**, 58–77.
Steinbauer, M., Dolos, K., Field, R., Reineking, B. & Beierkuhnlein, C. (2013) Re-evaluating the general dynamic theory of oceanic island biogeography. *Frontiers of Biogeography*, **5**, 185–194.
Steinbauer, M.J., Field, R., Fernández-Palacios, J.M., Irl, S.D.H., Otto, R., Schaefer, H. & Beierkuhnlein, C. (in press) Biogeographic ranges do not support niche theory in radiating Canary Island plant clades. *Global Ecology and Biogeography*.
Steinbauer, M.J., Field, R., Grytnes, J.-A., Trigas, P., Ah-Peng, C., Attorre, F., Birks, H.J.B., Borges, P.A.V., Cardoso, P., Chou, C.-H., De Sanctis, M., de Sequeira, m.M., Duarte, M.C., Elias, R.B., Fernández-Palácios, J.M., Gabriel, R., Gereau, R.E., Gillespie, R.G., Greimler, J., Harter, D.E.V., Huang, T.-J., Irl, S.D.H., Jeanmonod, D., Jentsch, A., Jump, A.S., Kueffer, C., Nogué, S., Otto, R., Price, J., Romeiras, M.M., Strsberg, D., Stuessy, T., Svenning, J.-C., Vetaas, O.R. & Beierkuhnlein, C. (in press b) Topography-driven isolation, speciation and a global increase of endemism with elevation. *Global Ecology and Biogeography*.
Sutherland, W.J., Freckleton, R.P., Godfray, H.C.J., Beissinger, S.R., Benton, T., Cameron, D.D., Carmel, Y., Coomes, D.A., Coulson, T., Emmerson, M.C., Hails, R.S., Hays, G.C., Hodgson, D.J., Hutchings, M.J., Johnson, D., Jones, J.P.G., Keeling, M.J., Kokko, H., Kunin, W.E., Lambin, X., Lewis, O.T., Malhi, Y., Mieszkowska, N., Milner-Gulland, E.J., Norris, K., Phillimore, A.B., Purves, D.W., Reid, J.M., Reuman, D.C., Thompson, K., Travis, J.M.J., Turnbull, L.A., Wardle, D.A. & Wiegand, T. (2013) Identification of 100 fundamental ecological questions. *Journal of Ecology*, **101**, 58–67.
Terborgh, J., Lopez, L., Nuñez, P., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G.H., Lambert, T.D. & Balbas, L. (2001) Ecological meltdown in predator-free forest fragments. *Science*, **294**, 1923–1926.
Traveset, A. & Richardson, D.M. (2006) Biological invasions as disruptors of plant reproductive mutualisms. *Trends in Ecology & Evolution*, **21**, 208–216.
Traveset, A., Tur, C., Trøjelsgaard, K., Heleno, R., Castro-Urgal, R. & Olesen, J.M. (in press) Global patterns of mainland and insular pollination networks. *Global Ecology and Biogeography.*
Traveset, A., Heleno, R., Chamorro, S., Vargas, P., McMullen, C.K., Castro-Urgal, R., Nogales, M., Herrera, H.W. & Olesen, J.M. (2013) Invaders of pollination networks in the Galápagos Islands: emergence of novel communities. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20123040.
Triantis, K.A., Borges, P.A.V., Ladle, R.J., Hortal, J., Cardoso, P., Gaspar, C., Dinis, F., Mendonça, E., Silveira, L.M.A., Gabriel, R., Melo, C., Santos, A.M.C., Amorim, I.R., Ribeiro, S.P., Serrano, A.R.M., Quartau, J.A. & Whittaker, R.J. (2010) Extinction debt on oceanic islands. *Ecography*, **33**, 285–294.

Triantis, K.A., Guilhaumon, F. & Whittaker, R.J. (2012) The island species–area relationship: biology and statistics. *Journal of Biogeography*, **39**, 215–231.

Trøjelsgaard, K. & Olesen, J.M. (2013) Macroecology of pollination networks. *Global Ecology and Biogeography*, **22**, 149–162.

Valente, L.M., Etienne, R.S. & Phillimore, A.B. (2014) The effects of island ontogeny on species diversity and phylogeny. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20133227.

Valente, L.M., Phillimore, A.B. & Etienne, R.S. (2015) Equilibrium and non-equilibrium dynamics simultaneously operate in the Galápagos islands. *Ecology Letters*, **18**, 844–852.

Van Der Wal, R., Truscott, A.-M., Pearce, I.S.K., Cole, L., Harris, M.P. & Wanless, S. (2008) Multiple anthropogenic changes cause biodiversity loss through plant invasion. *Global Change Biology*, **14**, 1428–1436.

Vargas, P., Heleno, R., Traveset, A. & Nogales, M. (2012) Colonization of the Galápagos Islands by plants with no specific syndromes for long-distance dispersal: a new perspective. *Ecography*, **35**, 33–43.

Wallace, A.R. (1880) *Island life*. Macmillan, London.

Warren, B.H., Simberloff, D., Ricklefs, R.E., Aguilée, R., Condamine, F.L., Gravel, D., Morlon, H., Mouquet, N., Rosindell, J., Casquet, J., Conti, E., Cornuault, J., Fernández-Palacios, J.M., Hengl, T., Norder, S.J., Rijsdijk, K.F., Sanmartín, I., Strasberg, D., Triantis, K.A., Valente, L.M., Whittaker, R.J., Gillespie, R.G., Emerson, B.C. & Thébaud, C. (2015) Islands as model systems in ecology and evolution: prospects fifty years after MacArthur–Wilson. *Ecology Letters*, **18**, 200–217.

Weigelt, P., Jetz, W. & Kreft, H. (2013) Bioclimatic and physical characterization of the world's islands. *Proceedings of the National Academy of Sciences*, **110**, 15307–15312.

Weigelt, P., Daniel Kissling, W., Kisel, Y., Fritz, S.A., Karger, D.N., Kessler, M., Lehtonen, S., Svenning, J.-C. & Kreft, H. (2015) Global patterns and drivers of phylogenetic structure in island floras. *Scientific Reports*, **5**, 12213.

Weigelt P., Steinbauer M.J., Sarmento Cabral J. & Kreft H. (2016) Late Quaternary climate change shapes island biodiversity. *Nature*, **532**, 99–102.

Weiher, E. & Keddy, P.A. (1995) Assembly rules, null models, and trait dispersion: new questions from old patterns. *Oikos*, **74**, 159–164.

Whittaker, R.J. & Fernández-Palacios, J.M. (2007) *Island bogeography: ecology, evolution, and conservation*, 2nd edn. Oxford University Press, Oxford.

Whittaker, R.J. & Triantis, K.A. (2012) The species–area relationship: an exploration of that 'most general, yet protean pattern'. *Journal of Biogeography*, **39**, 623–626.

Whittaker, R.J., Triantis, K.A. & Ladle, R.J. (2008) A general dynamic theory of oceanic island biogeography. *Journal of Biogeography*, **35**, 977–994.

Whittaker, R.J., Rigal, F., Borges, P.A.V., Cardoso, P., Terzopoulou, S., Casanoves, F., Pla, L., Guilhaumon, F., Ladle, R.J. & Triantis, K.A. (2014) Functional biogeography of oceanic islands and the scaling of functional diversity in the Azores. *Proceedings of the National Academy of Sciences*, **111**, 13709–13714.

Wilson, E.O. (1959) Adaptive shift and dispersal in a tropical ant fauna. *Evolution*, **13**, 122–144.

Wilson, E.O. (1961) The nature of the taxon cycle in the Melanesian ant fauna. *The American Naturalist*, **95**, 169–193.

Wilson, J. T. (1963) A possible origin of the Hawaiian Islands. *Canadian Journal of Physics*, **41**, 863–870.

Wright, D.H. (1983) Species–energy theory: an extension of species–area theory. *Oikos*, **41**, 496–506.

Box 1. Glossary

This glossary gives definitions of terms as we use them in the paper. Some of them (e.g. oceanic islands) have a range of definitions in the literature.

Adaptive radiation: the evolutionary process by which a single ancestral species diverges into an array of species that exhibit a wide range of ecological, phenotypic and behavioural diversity.

Alien species: a species that has been introduced in a new region outside its natural geographic range due to human actions (also known as exotic, exogenous, non-indigenous or non-native, among other terms).

Allopatric speciation: speciation that occurs when two populations are geographically isolated from each other, and originate distinct species.

*Archipelago: a g*roup of islands located reasonably close to each other, and that usually share a common geological origin.

Assembly rules: rules that describe the composition of biotas based on competition processes. These have been controversial.

Character displacement: the process by which traits of similar species diverge when such species co-occur geographically, as a consequence of competition scaling directly with similarity.

Checkerboard distributions: patterns presented by two or more ecologically similar species, where they have mutually exclusive and non-overlapping distributions.

Connectance: the proportion of all possible links that occur in a network.

Continental Island sensu lato*:* islands that have originated from the fragmentation (either recent – continental *sensu stricto.* or landbridge islands, or ancient – continental fragments) of the continental shelf and therefore have been connected to the continent in some point during its history. The fragmentation may result from sea-level rise or tectonic processes.

Density compensation: process leading to abnormally high abundance of species inhabiting islands with species-poor biotas.

Disharmony: the absence from an island of entire groups of species that would occur in continental settings.

Ecological release: expansion of the range, habitat and/or resource usage that occurs after a colonizing species enters an environment where natural enemies (competitors, parasites, predators) are missing.

Equilibrium Theory of Island Biogeography: a theoretical model by MacArthur and Wilson (1967) that postulates that the number of species present on an island will be determined by the dynamic relationship between immigration and extinction rates. In turn, immigration

rates depend greatly on the island isolation, while extinction rates are mainly associated with island area.

General Dynamic Model of oceanic island biogeography: a conceptual model by Whittaker *et al.* (2008) describing changes in diversity and ecological and evolutionary processes that are associated with the changes in the physiographic characteristics of volcanic oceanic islands (e.g. area, altitude) that occur throughout its ontogeny.

Habitat island: a discrete patch of habitat that is surrounded by a matrix of contrasting (usually unsuitable) habitat(s).

Hotspot archipelago: an archipelago of volcanic origin where islands are formed over near-stationary thermal plumes located in the Earth's upper mantel. Tectonic plate movements cause the islands to drift from that point, originating a series of islands of different ages.

Incidence functions: functions that describe how the probability of occurrence of a species varies with certain island characteristics (e.g. area, isolation, species richness).

Island ontogeny: the development of an island, from its formation through its development and subsequent degradation and disappearance.

Island rule: the tendency of small animals to evolve to larger sizes and large animals to evolve to smaller sizes on islands.

Mangrove islands: islands where the land area is mostly or totally below tidal water (at high tide), being overwash banks covered mainly by mangrove plants. They are usually located rather close to the mainland, and might, or might not, have been connected to the mainland coastal habitats.

Metacommunity: a group of communities that are linked through dispersal.

Metapopulation: a group of spatially separated populations that are connected by gene flow, extinction and recolonization.

Modularity: the occurrence of semi-independent groups (also called modules) of interacting species.

Nestedness (in respect to network analysis): a metric of the generalist–specialist balance in ecological communities. A network is nested when specialists interact with a subset of the group of species with which generalists interact.

Niche: the requirements (resources or physical conditions) of a population or species that allow it to survive in the focal certain area.

Oceanic Island: island formed due to volcanic activity, that has never been connected to another landmass. Upon their formation, oceanic islands are devoid of life, and so their biotas are assembled from colonization and/or speciation.

Parasitoid: an organism (usually an insect) that develops through adulthood by feeding on or in the body of a host (usually an arthropod), eventually killing it.

Priority effects: the effects that the first species that colonize an area cause on the subsequent colonizers, as a result of colonizing first.

Sympatric speciation: speciation that occurs when populations are not geographically isolated from each other.

Target effect: the increased probability that a larger island has of being colonized than a smaller one, resulting from random dispersal.

Taxon cycle: sequential phases of expansion and contraction of species' ranges, which are usually associated with shifts in the species' ecological niches.

True island: a piece of land that is surrounded by water.

Table 1. A non-exhaustive summary of theories, processes and patterns that a) have originated in island studies, or b) have not originated from island studies, but have received an important theoretical and/or analytical input from island studies. Examples (citations) of each theory, process or pattern are given for different types of island (see Box 1), and also for mainland systems. Many of these examples (indicated by #) are not exclusive to one particular theory, process or pattern, and could indeed also be included in one or more different sections. * indicates the studies that are part of this special issue. See Appendix 1 (Data Sources) for references not in the main reference list. The expanded online version of this table (Table S1) additionally categorizes the examples by taxon.

Appendix 1 – Data sources

List of references for the examples cited in Table 1 and Table S1 that are not in the main reference list.

Supplementary Material (online only)

Table S1.

Expanded version of Table 1. A non-exhaustive summary of theories, processes and patterns that a) have originated in island studies, or b) have not originated from island studies, but have received an important theoretical and/or analytical input from island studies. Examples (citations) of each theory, process or pattern are given for different types of island (see Box 1, main paper), and also for mainland systems. Many of these examples (indicated by #) are not exclusive to one particular theory, process or pattern, and could indeed also be included in one or more different sections. The main taxa used in each example are displayed in the columns. Symbols are as follows: $f(x)$ - Theoretical study (no use, or very limited use, of empricial data);  - Arthropods;  - Other terrestrial invertebrates;  - Mammals;  - Reptiles;  - Amphibians;  - Birds;  - Fish;  - Marine invertebrates;  - Plants;  - Microorganisms. * indicates the studies that are part of this special issue. See main paper for references: main reference list and Appendix 1 (Data Sources).

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Theories/Patterns that have originated mainly from island studies

Adaptive radiation

** Oceanic Islands*: * Algar *et al*., this issue; Blonder *et al.*, 2016; Gillespie *et al.*, 2004; Givnish *et al*., 2009; Grant & Grant, 2008; Losos, 2011; Pinto *et al*., 2008[#]
Continental Islands: Baldwin, 2007; van der Geer *et al.,* 2010
Habitat Islands: Dawson & Hammer, 2005; Seehausen, 2006
Non-Island Systems: Hughes *et al.*, 2006; Pincheira-Donoso *et al.*, 2015

Ecological release and Density compensation

** Oceanic Islands*: Grant & Grant, 2006; Lack, 1947; Novosolov *et al.*, 2016 [#]; Schluter, 1988; * Steinbauer *et al.*, this issue; Wright, 1980 [#]
Continental Islands: Barun *et al*., 2015; Case, 1975; Lomolino, 1984; MacArthur, 1972; Schluter & McPhail, 1992; Schoener & Spiller, 1987
Habitat Islands: Hobbs *et al.*, 2012; Martin & Pfennig, 2011; McGrady-Steed & Morin, 2000
Non-Island Systems: Adams & Rohlf, 2000; Davies *et al.*, 2007; Schmitt & Holbrook, 1990

Body size evolution and the "island rule"

Oceanic Islands: Clegg & Owens, 2002; Lomolino, 2005 [#]
Continental Islands: Lawlor, 1982; Meiri, 2007; Montesinos *et al.*, 2012
Habitat Islands: Schmidt & Jensen, 2003
Non-Island Systems: McClain *et al.*, 2006

Taxon cycle

Oceanic Islands: Economo *et al.*, 2012; Jønsson *et al.*, 2014 [#]; Ricklefs & Bermingham, 2002; Ricklefs & Cox, 1972; Wilson, 1961
Non-Island Systems: Economo *et al.*, 2015; Erwin, 1985; Glazier, 1980; Hoagstrom *et al.*, 2014

Equilibrium Theory of Island Biogeography

** Oceanic Islands*: * Fernández-Palacios *et al.*, this issue; Heaney, 2000 [#]; MacArthur & Wilson, 1963, 1968; Rosindell & Harmon, 2013 [#]
Continental Islands: Cody, 2006; Foufopoulos & Mayer, 2007; Jones & Diamond, 1976
Mangrove Islands: Simberloff & Wilson, 1969, 1970
** Habitat Islands*: Bossard, 2014; Brown, 1971, 1978; * Dawson, this issue; Hart & Pearson, 2011; March & Bass, 1995; Schoener, 1974; Smith, 1979
Non-Island Systems: Rosenzweig, 1975 [#]

General Dynamic Model of Island Biogeography

** Oceanic Islands*: Borges & Hortal, 2009; * Borregaard *et al.*, this issue; Bunnefeld & Phillimore, 2012; Cameron *et al.*, 2013; Fattorini, 2009; Steinbauer *et al.*, 2013; Valente *et al.*, 2014; Whittaker *et al.*, 2008

Asssembly rules, Checkerboard distributions and Null models in ecology

** Oceanic Islands:* Connor & Simberloff, 1979; Connor *et al.*, 2013; Diamond, 1975a; Gotelli, 2000 [#]; Mayr & Diamond, 2001; * Santos *et al.*, this issue [#]; Simberloff & Collins, 2009
Continental Islands: Cody, 2006
Habitat Islands: Englund *et al.*, 2009
Non-Island Systems: Gotelli & Ellison, 2002; Gotelli & Graves, 1996; Gotelli *et al.*, 1997; Rautenbach *et al.*, 2014; Sanders *et al.*, 2007

Unified Neutral Theory of Biodiversity and Biogeography

Oceanic Islands: Rosindell & Phillimore, 2011 [#]
Continental Islands: Hubbell, 2001, 2009
Habitat Islands: Dornelas *et al*., 2006; Gilbert *et al.*, 2006
Non-Island Systems: Ricklefs, 2006; Rosindell *et al.*, 2015

Theories/patterns not originated on island systems, but that have benefited from them

Natural Selection and Speciation

Oceanic Islands: Calsbeek & Cox, 2010; Darwin, 1859; Grant & Grant , 2008, 2016; Roderick & Gillespie, 1998; Rowe *et al.*, 2016 [#]; Savolainen *et al.*, 2006;

Stuessy *et al.*, 2006

Continental Islands: Clegg *et al.*, 2002 #; Comes *et al.*, 2008; Lescak *et al.*, 2015

Habitat Islands: Barluenga *et al.*, 2006; Gao *et al.*, 2015; Juan *et al*., 2010

Long distance dispersal and Colonization Routes

Oceanic Islands: Carlquist, 1966 #; Heleno & Vargas, 2015; Nathan, 2006 #; Vargas *et al.*, 2012; Wada *et al.*, 2012

Continental Islands: Ali & Huber, 2000; Alsos *et al.*, 2015

Habitat Islands: Huth *et al.*, 2015

Non-Island Systems: Bellemain & Ricklefs, 2008 #; Brochet *et al*., 2009; Dawson & Hammer, 2008 #; Nicholson *et al.*, 2005 #; O'Grady & DeSalle, 2008 #; Patiño *et al.,* 2015 #

Species-area relationship

Oceanic Islands: Aranda *et al.*, 2013; Kisel *et al.*, 2010 #; Lomolino & Weiser, 2001 #; Losos & Schluter, 2000; Ricklefs & Lovette, 1999; Santos *et al.*, 2010 #; Scheiner, 2003 #; Triantis *et al.*, 2012 #; Wright, 1983 #

** Continental Islands*: Holt et al., 1999 #; Kurt & Howe, 1979; Panitsa et al., 2006; Roslin *et al.*, 2014; * Schoener *et al.*, this issue; Sfenthourakis, 1996

** Habitat Islands*: Brown & Dinsmore, 1988; Belmaker *et al.*, 2007; Hanski *et al.*, 2013; He & Hubbel, 2011; Krauss *et al.*, 2003; * Matthews *et al.*, this issue #; Newmark, 1986; Wagner *et al.*, 2014

Non-Island Systems: Kisel *et al.*, 2011; Qian *et al.*, 2007; Storch *et al.*, 2012

Nestedness patterns

Oceanic Islands: Cook & Quinn, 1995 #; Darlington, 1957 #; Florencio *et al*., 2015 #

Continental Islands: Azeria, 2004; Conroy *et al.*, 1999; Dennis *et al.*, 2012; Murakami & Hirao, 2010; Wang *et al.*, 2010

Habitat Islands: Matthews *et al.*, 2015; Patterson & Atmar, 1986 #; Watling & Donnelly, 2006 #

Non-Island Systems: Baselga, 2010

Metapopulation dynamics

Oceanic Islands: Farrington & Petren, 2011; Garcia-Verdugo *et al.*, 2010; Inchaisti & Weimerskirch, 2002 #

Continental Islands: Hanski, 2009 #; Nieminen, 1996; Nieminen & Hanski, 1998; Zalewski, 2004
Habitat Islands: Bay *et al*., 2008; Hanski & Ovaskainen, 2000
Non-Island Systems: Levins, 1969, 1970

Ecological Succession

Oceanic Islands: Edwards & Thorton, 2001; Magnússon *et al.*, 2014; Mueller-Dombois & Bohemer, 2013; Thornton *et al*., 1993; Whitaker *et al.*, 1989
Continental Islands: Lavoie & Filion, 2001; Rydin & Borgegård, 1988
Mangrove Islands: Piechnick *et al., 2008*
Habitat Islands: McClanahan, 2014; Pinotti *et al.*, 2015
Non-Island Systems: Clements, 1916; Dauber & Wolters, 2005; Letcher, 2010

Trophic Theory and Interaction Networks

** Oceanic Islands*: González-Castro *et al.*, 2012 #; * Nogales *et al.*, this issue; Olesen *et al.*, 2002; * Rominger *et al.*, this issue; * Traveset *et al.*, this issue #
Continental Islands: Strong & Leroux, 2014; Terborgh, 2009 #; Terborgh *et al.*, 2001
** Mangrove Islands*: * Cirtwill & Stouffer, this issue; Gravel *et al.*, 2011 #
Habitat Islands: Harvey & MacDougall, 2014; Holt, 2009 #; Tscharntke & Brandl, 2004
Non-Island Systems: Amaresakare, 2008; Pimm, 1982

Conservation Theory - Invasive species, Extinction and Habitat fragmentation

** Oceanic Islands*: Bellard *et al*., 2014 #; * Blackburn *et al*., this issue #; Boyer *et al.*, 2014 #; Coblentz, 1978 #; Duncan *et al.*, 2013 #; Kueffer *et al.*, 2010 #; Sax *et al.*, 2002 #; Triantis *et al.*, 2010; Walsh *et al.*, 2013 #
Continental Islands: Gasc *et al.*, 2010; Pattermore & Wilcove, 2012; Pretto *et al.*, 2012; van de Crommenacker *et al.*, 2015
Habitat Islands: Diamond, 1975b, 1981; Krauss *et al.*, 2010; Larsen *et al*., 2005 #; Laurence, 2009; Lindenmayer, 2015; Simberlogg & Abele, 1976; Tjørve, 2010

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Appendix 1 – Data sources

List of references for the examples cited in Table 1 and Table S1 that are not in the main reference list.

Adams, D.C. & Rohlf, F.J. (2000) Ecological character displacement in *Plethodon*: Biomechanical differences found from a geometric morphometric study. *Proceedings of the National Academy of Sciences*, **97**, 4106–4111.

Ali, J.R. & Huber, M. (2010) Mammalian biodiversity on Madagascar controlled by ocean currents. *Nature*, **463**, 653–656.

Alsos, I.G., Ehrich, D., Eidesen, P.B., Solstad, H., Westergaard, K.B., Schönswetter, P., Tribsch, A., Birkeland, S., Elven, R. & Brochmann, C. (2015) Long-distance plant dispersal to North Atlantic islands: colonization routes and founder effect. *AoB Plants*, **7**, plv036.

Amarasekare, P. (2008) Spatial dynamics of foodwebs. *Annual Review of Ecology, Evolution, and Systematics*, **39**, 479–500.

Aranda, S.C., Gabriel, R., Borges, P.A.V., Santos, A.M.C., Hortal, J., Baselga, A. & Lobo, J.M. (2013) How do different dispersal modes shape the species–area relationship? Evidence for between-group coherence in the Macaronesian flora. *Global Ecology and Biogeography*, **22**, 483–493.

Azeria, E.T. (2004) Terrestrial bird community patterns on the coralline islands of the Dahlak Archipelago, Red Sea, Eritrea. *Global Ecology and Biogeography*, **13**, 177–187.

Baldwin, B.G. (2007) Adaptive radiation of shrubby tarweeds (*Deinandra*) in the California Islands parallels diversification of the Hawaiian silversword alliance (Compositae-Madiinae). *American Journal of Botany*, **94**, 237–248.

Barluenga, M., Stölting, K.N., Salzburger, W., Muschick, M. & Meyer, A. (2006) Sympatric speciation in Nicaraguan crater lake cichlid fish. *Nature*, **439**, 719–723.

Barun, A., Simberloff, D., Meiri, S., Tvrtković, N. & Tadić, Z. (2015) Possible character displacement of an introduced mongoose and native marten on Adriatic Islands, Croatia. *Journal of Biogeography*, **42**, 2257–2269.

Baselga, A. (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, **19**, 134–143.

Bay, L.K., Caley, M.J. & Crozier, R.H. (2008) Meta-population structure in a coral reef fish demonstrated by genetic data on patterns of migration, extinction and re-colonisation. *BMC Evolutionary Biology*, **8**, 1–17.

Belmaker, J., Ben-Moshe, N., Ziv, Y. & Shashar, N. (2007) Determinants of the steep species-area relationship of coral reef fishes. *Coral Reefs*, **26**, 103–112.

Blonder, B., Baldwin, B.G., Enquist, B.J. & Robichaux, R.H. (2016) Variation and macroevolution in leaf functional traits in the Hawaiian silversword alliance (Asteraceae). *Journal of Ecology*, **104**, 219–228.

Bossard, R.L. (2014) Flea (Siphonaptera) species richness in the Great Basin Desert and island biogeography theory. *Journal of Vector Ecology*, **39**, 164–167.

Brochet, A.-L., Guillemain, M., Fritz, H., Gauthier-Clerc, M. & A.J., G. (2009) The role of migratory ducks in the long-distance dispersal of native plants and the spread of exotic plants in Europe. *Ecography*, **32**, 919–928.

Brown, M. & Dinsmore, J.J. (1988) Habitat islands and the equilibrium theory of island biogeography: testing some predictions. *Oecologia*, **75**, 426–429.

Calsbeek, R. & Cox, R.M. (2010) Experimentally assessing the relative importance of predation and competition as agents of selection. *Nature*, **465**, 613–616.

Cameron, R.A.D., Triantis, K.A., Parent, C.E., Guilhaumon, F., Alonso, M.R., Ibáñez, M., de Frias Martins, A.M., Ladle, R.J. & Whittaker, R.J. (2013) Snails on oceanic islands: testing the general dynamic model of oceanic island biogeography using linear mixed effect models. *Journal of Biogeography*, **40**, 117–130.

Carlquist, S. (1966) The biota of long-distance dispersal. I. Principles of dispersal and evolution. *The Quarterly Review of Biology*, **41**, 247–270.

Case, T.J. (1975) Species numbers, density compensation, and colonizing ability of lizards on islands in the Gulf of California. *Ecology*, **56**, 3–18.

Clegg, S.M. & Owens, I.P.F. (2002) The 'island rule' in birds: medium body size and its ecological explanation. *Proceedings of the Royal Society B*, **269**, 1359–1365.

Clegg, S.M., Degnan, S.M., Moritz, C., Estoup, A., Kikkawa, J. & Ian, P.F.O. (2002) Microevolution in island forms: the roles of drift and directional selection in morphological divergence of a passerine bird. *Evolution*, **56**, 2090–2099.

Clements, F.E. (1916) *Plant succession: analysis of the development of vegetation*. Carnegie Institution of Washington Publications, Washington.

Cody, M.L. (2006) *Plants on islands. Diversity and dynamics on a continental archipelago*. University of California Press, Berkeley and Los Angeles.

Comes, H.P., Tribsch, A. & Bittkau, C. (2008) Plant speciation in continental island floras as exemplified by Nigella in the Aegean Archipelago. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **363**, 3083–3096.

Connor, E.F., Collins, M.D. & Simberloff, D. (2013) The checkered history of checkerboard distributions. *Ecology*, **94**, 2403–2414.

Conroy, C.J., Demboski, J.R. & Cook, J.A. (1999) Mammalian biogeography of the Alexander Archipelago of Alaska: a north temperate nested fauna. *Journal of Biogeography*, **26**, 343–352.

Cook, R.R. & Quinn, J.F. (1995) The influence of colonization in nested species subsets. *Oecologia*, **102**, 413–424.

Darlington, P.J. (1957) *Zoogeography: the geographical distribution of animals*. Wiley, New York.

Darwin, C. (1859) *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*, First edition edn. John Murray, London.

Dauber, J. & Wolters, V. (2005) Colonization of temperate grassland by ants. *Basic and Applied Ecology*, **6**, 83–91.

Davies, T.J., Meiri, S., Barraclough, T.G. & Gittleman, J.L. (2007) Species co-existence and character divergence across carnivores. *Ecology Letters*, **10**, 146–152.

Dawson, M.N. & Hamner, W.M. (2005) Rapid evolutionary radiation of marine zooplankton in peripheral environments *Proceedings of the National Academy of Sciences*, **102**, 9235–9240.

Dawson, M.N. & Hamner, W.M. (2008) A biophysical perspective on dispersal and the geography of evolution in marine and terrestrial systems. *Journal of the Royal Society Interface*, **5**, 135–150.

Dennis, R.L.H., Hardy, P.B. & Dapporto, L. (2012) Nestedness in island faunas: novel insights into island biogeography through butterfly community profiles of colonization ability and migration capacity. *Journal of Biogeography*, **39**, 1412-1426.

Diamond, J.M. (1975) The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation*, **7**, 129–146.

Diamond, A.W. (1981) Reserves as oceanic islands: lessons for conserving some East African montane forests. *African Journal of Ecology*, **19**, 21–25.

Dornelas, M., Connolly, S.R. & Hughes, T.P. (2006) Coral reef diversity refutes the neutral theory of biodiversity. *Nature*, **440**, 80–82.

Economo, E.P., Sarnat, E.M., Janda, M., Clouse, R., Klimov, P.B., Fischer, G., Blanchard, B.D., Ramirez, L.N., Andersen, A.N., Berman, M., Guénard, B., Lucky, A., Rabeling, C., Wilson, E.O. & Knowles, L.L. (2015) Breaking out of biogeographical modules: range expansion and taxon cycles in the hyperdiverse ant genus *Pheidole*. *Journal of Biogeography*, **42**, 2289–2301.

Edwards, J.S. & Thornton, I.W.B. (2001) Colonization of an island volcano, Long Island, Papua New Guinea, and an emergent island, Motmot, in its caldera lake. IV. The pioneer arthropod community of Motmot. *Journal of Biogeography*, **28**, 1379–1388.

Englund, G., Johansson, F., Olofsson, P., Salonsaari, J. & Öhman, J. (2009) Predation leads to assembly rules in fragmented fish communities. *Ecology Letters*, **12**, 663–671.

Farrington, H.L. & Petren, K. (2011) A century of genetic change and metapopulation dynamics in the Galápagos warbler finches ("Certhidea"). *Evolution*, **65**, 3148–3161.

Fattorini, S. (2009) On the general dynamic model of oceanic island biogeography. *Journal of Biogeography*, **36**, 1100–1110.

Florencio, M., Lobo, J.M., Cardoso, P., Almeida-Neto, M. & Borges, P.A.V. (2015) The colonisation of exotic species does not have to trigger faunal homogenisation: lessons from the assembly patterns of arthropods on oceanic islands. *PLos ONE*, **10**, e0128276.

Foufopoulos, J. & Mayer, G.C. (2007) Turnover of passerine birds on islands in the Aegean Sea (Greece). *Journal of Biogeography*, **34**, 1113–1123.

Gao, Y., Ai, B., Kong, H., Kang, M. & Huang, H. (2015) Geographical pattern of isolation and diversification in karst habitat islands: a case study in the *Primulina eburnea* complex. *Journal of Biogeography*, **42**, 2131–2144.

Garcia-Verdugo, C., Forrest, A.D., Fay, M.F. & Vargas, P. (2010) The relevance of gene flow in metapopulation dynamics of an oceanic island endemic, *Olea europaea* sbsp. *guanchica*. *Evolution*, **64**, 3525–3536.

Gasc, A., Duryea, M.C., Cox, R.M., Kern, A. & Calsbeek, R. (2010) Invasive predators deplete genetic diversity of island lizards. *PLos ONE*, **5**, e12061.

Gilbert, B., Laurance, W.F., Leigh Jr., E.G. & Nascimento, H.E.M. (2006) Can neutral theory predict the responses of Amazonian tree communities to forest fragmentation? *The American Naturalist*, **168**, 304–317.

Gillespie, R. (2004) Community assembly through adaptative radiation in Hawaiian spiders. *Science*, **303**, 356–359.

Gotelli, N.J. (2000) Null model analysis of species co-occurrence patterns. *Ecology*, **81**, 2606–2621.

Gotelli, N.J. & Ellison, A.M. (2002) Assembly rules for New England ant assemblages. *Oikos*, **99**, 591–599.

Gotelli, N.J., Buckley, N.J. & Wiens, J.A. (1997) Co-occurrence of Australian land birds: Diamond's assembly rules revisited. *Oikos*, **80**, 311–324.

Grant, P.R. & Grant, B.R. (2016) Introgressive hybridization and natural selection in Darwin's finches. *Biological Journal of the Linnean Society*, **117**, 812–822.

Hanski, I. (2009) The theories of island biogeography and metapopulation dynamics - science marches forward but the legacy of good ideas lasts for a long time. *The*

theory of island biogeography revisited (ed. by J.B. Losos and R. Ricklefs), pp. 186–213. Princeton University Press, Princeton, NJ.

Hanski, I. & Ovaskainen, O. (2000) The metapopulation capacity of a fragmented landscape. *Nature*, **404**, 755–758.

Hanski, I., Zurita, G.A., Bellocq, M.I. & Rybicki, J. (2013) Species-fragmented area relationship. *Proceedings of the National Academy of Sciences*, **110**, 12715–12720.

Hart, P.J.B. & Pearson, E. (2011) An application of the theory of island biogeography to fish speciation on seamounts. *Marine Ecology Progress Series*, **430**, 281-288.

Harvey, E. & MacDougall, A.S. (2014) Trophic island biogeography drives spatial divergence of community establishment. *Ecology*, **95**, 2870–2878.

He, F. & Hubbell, S.P. (2011) Species–area relationships always overestimate extinction rates from habitat loss. *Nature*, **473**, 368–371.

Heaney, L.R. (2000) Dynamic disequilibrium: a long-term, large-scale perspective on the equilibrium model of island biogeography. *Global Ecology and Biogeography*, **9**, 59–74.

Hoagstrom, C.W., Ung, V. & Taylor, K. (2014) Miocene rivers and taxon cycles clarify the comparative biogeography of North American highland fishes. *Journal of Biogeography*, **41**, 644–658.

Hobbs, J.-P.A., Jones, G.P., Munday, P.L., Connolly, S.R. & Srinivasan, M. (2012) Biogeography and the structure of coral reef fish communities on isolated islands. *Journal of Biogeography*, **39**, 130–139.

Holt, R.D., Lawton, J.H., Polis, G.A. & Martinez, N.D. (1999) Trophic rank and the species-area relationship. *Ecology*, **80**, 1495–1504.

Hubbell, S.P. (2009) Neutral theory and the theory of island biogeography. *The Theory of Island Biogeography Revisited,* (ed. by J.L.a.R.E. Ricklefs), pp. 264–282. Princeton Univ. Press Princeton, NJ

Hughes, C. & Eastwood, R. (2006) Island radiation on a continental scale: Exceptional rates of plant diversification after uplift of the Andes. *Proceedings of the National Academy of Sciences*, **103**, 10334–10339.

Huth, G., Haegeman, B., Pitard, E. & Munoz, F. (2015) Long-distance rescue and slow extinction dynamics govern multiscale metapopulations. *The American Naturalist*, **186**, 460–469.

Inchaisti, P. & Weimerskirch, H. (2002) Dispersal and metapopulation dynamics of an oceanic seabird, the wandering albatross, and its consequences for its response to long-line fisheries. *Journal of Animal Ecology*, **71**, 765–770.

Jones, H.L. & Diamond, J.M. (1976) Short-time-base studies of turnover in breeding bird populations on the California Channel Islands. *Condor*, **78**, 526–549.

Juan, C., Guzik, M.T., Jaume, D. & Cooper, S.J.B. (2010) Evolution in caves: Darwin's wrecks of ancient life in the molecular era. *Molecular Ecology*, **19**, 3865–3880.

Kisel, Y. & Barraclough, T.G. (2010) Speciation has a spatial scale that depends on levels of gene flow. *The American Naturalist*, **175**, 316–334.

Kisel, Y., McInnes, L., Toomey, N.H. & Orme, C.D.L. (2011) How diversification rates and diversity limits combine to create large-scale species–area relationships. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **366**, 2514–2525.

Krauss, J., Steffan-Dewenter, I. & Tscharntke, T. (2003) How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? *Journal of Biogeography*, **30**, 889–900.

Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R.K., Helm, A., Kuussaari, M., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Pöyry, J., Raatikainen, K.M., Sang, A., Stefanescu, C., Teder, T., Zobel, M. & Steffan-Dewenter, I. (2010) Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecology Letters*, **13**, 597–605.

Kueffer, C., Daehler, C.C., Torres-Santana, C.W., Lavergne, C., Meyer, J.-Y., Otto, R. & Silva, L. (2010) A global comparison of plant invasions on oceanic islands. *Perspectives in Plant Ecology, Evolution and Systematics*, **12**, 145–161.

Kurt, A.R. & Howe, R.W. (1979) Species-area relations of birds on small islands in a Minnesota lake. *Evolution*, **33**, 468–477.

Lack, D. (1947) *Darwin's Finches*. Cambridge University Press.

Larsen, T.H., Williams, N.M. & Kremen, C. (2005) Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letters*, **8**, 538–547.

Lavoie, M. & Filion, L. (2001) Holocene vegetation dynamics of Anticosti Island, Québec, and consequences of remoteness on ecological succession. *Quaternary Research*, **56**, 112–127.

Lawlor, T.E. (1982) The Evolution of Body Size in Mammals: Evidence from Insular Populations in Mexico. *The American Naturalist*, **119**, 54–72.

Lescak, E.A., Bassham, S.L., Catchen, J., Gelmond, O., Sherbick, M.L., von Hippel, F.A. & Cresko, W.A. (2015) Evolution of stickleback in 50 years on earthquake-uplifted islands. *Proceedings of the National Academy of Sciences*, **112**, E7204–E7212.

Letcher, S.G. (2010) Phylogenetic structure of angiosperm communities during tropical forest succession. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 97–104.

Levins, R. (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, **15**, 237–240.

Levins, R. (1970) Extinction. *Lecture Notes in Mathematics*, **2**, 75–107.

Lindenmayer, D.B., Wood, J., McBurney, L., Blair, D. & Banks, S.C. (2015) Single large versus several small: The SLOSS debate in the context of bird responses to a variable retention logging experiment. *Forest Ecology and Management*, **339**, 1–10.

Lomolino, M.V. (1984) Immigrant selection, predation, and the distributions of *Microtus pennsylvanicus* and *Blarina brevicauda* on islands. *The American Naturalist*, **123**, 468–483.

Lomolino, M.V. (2005) Body size evolution in insular vertebrates: generality of the island rule. *Journal of Biogeography*, **32**, 1683–1699.

Lomolino, M.V. & Weiser, M.D. (2001) Towards a more general species-area relationship: diversity on all islands, great and small. *Journal of Biogeography*, **28**, 431–445.

Magnússon, B., Magnússon, S.H., Ólafsson, E. & Sigurdsson, B.D. (2014) Plant colonization, succession and ecosystem development on Surtsey with reference to neighbouring islands. *Biogeosciences*, **11**, 5521–5537.

Martin, R.A. & Pfennig, D.W. (2011) Evaluating the targets of selection during character displacement. *Evolution*, **65**, 2946–2958.

Matthews, T.J., Sheard, C., Cottee-Jones, H.E.W., Bregman, T.P., Tobias, J.A. & Whittaker, R.J. (2015) Ecological traits reveal functional nestedness of bird communities in habitat islands: a global survey. *Oikos*, **124**, 817-826.

Mayr, E. & Diamond, J. (2001) *The birds of Northern Melanesia. Speciation, ecology & biogeography*. Oxford University Press, New York.

McClain, C.R., Boyer, A.G. & Rosenberg, G. (2006) The island rule and the evolution of body size in the deep sea. *Journal of Biogeography*, **33**, 1578–1584.

McClanahan, T.R. (2014) Decadal coral community reassembly on an African fringing reef. *Coral Reefs*, **33**, 939–950.

McGrady-Steed, J. & Morin, P.J. (2000) Biodiversity, density compensation, and the dynamics of populations and functional groups. *Ecology*, **81**, 361–373.

Meiri, S. (2007) Size evolution in island lizards. *Global Ecology and Biogeography*, **16**, 702–708.

Montesinos, R., da Silva, H.R. & de Carvalho, A.L.G. (2012) The 'island rule' acting on anuran populations (Bufonidae: *Rhinella ornata*) of the southern hemisphere. *Biotropica*, **44**, 506-511.

Mueller-Dumbois, D. & Boehmer, H.J. (2013) Origin of the Hawaiian rainforest and its transition states in long-term primary succession. *Biogeosciences*, **10**, 5171–5182.

Nathan, R. (2006) Long-distance dispersal of plants. *Science*, **313**, 786–788.

Murakami, M. & Hirao, T. (2010) Nestedness of insect assemblages on small Bahamian islands: importance of spatial processes. *Insect Conservation and Diversity*, **3**, 229–235.

Newmark, W.D. (1986) Species-area relationship and its determinants for mammals in western North American national parks. *Biological Journal of the Linnean Society*, **28**, 83–98.

Nicholson, K.E., Glor, R.E., Kolbe, J.J., Larson, A., Blair Hedges, S. & Losos, J.B. (2005) Mainland colonization by island lizards. *Journal of Biogeography*, **32**, 929–938.

Nieminen, M. (1996) Migration of moth species in a network of small islands. *Oecologia*, **108**, 643–651.

Nieminen, M. & Hanski, I. (1998) Metapopulations of moths on islands: a test of two contrasting models. *Journal of Animal Ecology*, **67**, 149–160.

Novosolov, M., Rodda, G.H., Feldman, A., Kadison, A.E., Dor, R. & Meiri, S. (2016) Power in numbers. Drivers of high population density in insular lizards. *Global Ecology and Biogeography*, **25**, 87–95.

O'Grady, P. & DeSalle, R. (2008) Out of Hawaii: the origin and biogeography of the genus *Scaptomyza* (Diptera: Drosophilidae). *Biology Letters*, **4**, 195–199.

Panitsa, M., Tzanoudakis, D., Triantis, K.A. & Sfenthourakis, S. (2006) Patterns of species richness on very small islands: the plants of the Aegean archipelago. *Journal of Biogeography*, **33**, 1223–1234.

Pattemore, D.E. & Wilcove, D.S. (2012) Invasive rats and recent colonist birds partially compensate for the loss of endemic New Zealand pollinators. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 1597–1605.

Patterson, B.D. & Atmar, W. (1986) Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biological Journal of the Linnean Society*, **28**, 65–82.

Piechnik, D.A., Lawler, S.P. & Martinez, N.D. (2008) Food-web assembly during a classic biogeographic study: species' "trophic breadth" corresponds to colonization order. *Oikos*, **117**, 665–674.

Pimm, S.L. (1982) *Food webs*. The University of Chicago Press, London.
Pincheira-Donoso, D., Harvey, L.P. & Ruta, M. (2015) What defines an adaptive radiation? Macroevolutionary diversification dynamics of an exceptionally species-rich continental lizard radiation. *BMC Evolutionary Biology*, **15**, 153.
Pinotti, B.T., Pagotto, C.P. & Pardini, R. (2015) Wildlife recovery during tropical forest succession: assessing ecological drivers of community change. *Biotropica*, **47**, 765–774.
Pretto, F., Celesti-Grapow, L., Carli, E., Brundu, G. & Blasi, C. (2012) Determinants of non-native plant species richness and composition across small Mediterranean islands. *Biological Invasions*, **14**, 2559–2572.
Qian, H., Fridley, J.D. & Palmer, M.W. (2007) The latitudinal gradient of species-area relationships for vascular plants of North America. *The American Naturalist*, **170**, 690–701.
Rautenbach, A., Dickerson, T. & Schoeman, M.C. (2014) Diversity of rodent and shrew assemblages in different vegetation types of the savannah biome in South Africa: no evidence for nested subsets or competition. *African Journal of Ecology*, **52**, 30–40.
Ricklefs, R.E. & Cox, G.W. (1972) Taxon cycles in the West Indian avifauna. *The American Naturalist*, **106**, 195–219.
Ricklefs, R.E. & Lovette, I.J. (1999) The roles of island area *per se* and habitat diversity in the species-area relationships of four Lesser Antillean faunal groups. *Journal of Animal Ecology*, **68**, 1142–1160.
Roderick, G.K. & Gillespie, R.G. (1998) Speciation and phylogeography of Hawaiian terrestrial arthropods. *Molecular Ecology*, **7**, 519–531.
Rosindell, J., Harmon, L.J. & Etienne, R.S. (2015) Unifying ecology and macroevolution with individual-based theory. *Ecology Letters*, **18**, 472–482.
Rowe, K.C., Achmadi, A.S. & Esselstyn, J.A. (2016) Repeated evolution of carnivory among Indo-Australian rodents. *Evolution*, **70**, 653–665.
Rydin, H. & Borgegård, S.-O. (1988) Plant species richness on islands over a century of primary succession: Lake Hjälmaren. *Ecology*, **69**, 916–927.
Sanders, N.J., Gotelli, N.J., Wittman, S.E., Ratchford, J.S., Ellison, A.M. & Jules, E.S. (2007) Assembly rules of ground-foraging ant assemblages are contingent on disturbance, habitat and spatial scale. *Journal of Biogeography*, **34**, 1632–1641.
Savolainen, V., Anstett, M.-C., Lexer, C., Hutton, I., Clarkson, J.J., Norup, M.V., Powell, M.P., Springate, D., Salamin, N. & Baker, W.J. (2006) Sympatric speciation in palms on an oceanic island. *Nature*, **441**, 210–213.
Scheiner, S.M. (2003) Six types of species-area curves. *Global Ecology and Biogeography*, **12**, 441–447.
Schluter, D. (1988) Character displacement and the adaptive divergence of finches on islands and continents. *The American Naturalist*, **131**, 799–824.
Schluter, D. & McPhail, J.D. (1992) Ecological Character Displacement and Speciation in Sticklebacks. *The American Naturalist*, **140**, 85–108.
Schmidt, N.M. & Jensen, P.M. (2003) Changes in mammalian body length over 175 years—adaptations to a fragmented landscape? *Conservation Ecology*, **7**, 6.
Schmitt, R.J. & Holbrook, S.J. (1990) Population responses of surfperch released from competition. *Ecology*, **71**, 1653–1665.
Schoener, A. (1974) Experimental zoogeography: colonization of marine mini-islands. *The American Naturalist*, **108**, 715–738.

Schoener, T.W. & Spiller, D.A. (1987) Effect of lizards on spider populations: manipulative reconstruction of a natural experiment. *Science*, **236**, 949–952.

Seehausen, O. (2006) African cichlid fish: a model system in adaptive radiation research. *Proceedings of the Royal Society of London B: Biological Sciences*, **273**, 1987–1998.

Sfenthourakis, S. (1996) The species-area relationship of terrestrial isopods (Isopoda; Oniscidea) from the Aegean archipelago (Greece): a comparative study. *Global Ecology and Biogeography Letters*, **5**, 149–157.

Simberloff, D. & Wilson, E.O. (1969) Experimental zoogeography of islands: the colonization of empty islands. *Ecology*, **50**, 278–296.

Simberloff, D. & Wilson, E.O. (1970) Experimental zoogeography of islands. A two-year record of colonization. *Ecology*, **51**, 934–937.

Simberloff, D.S. & Abele, L.G. (1976) Island biogeography theory and conservation practice. *Science*, **191**, 285–286.

Smith, G.B. (1979) Relationship of eastern gulf of Mexico reef-fish communities to the species equilibrium theory of insular biogeography. *Journal of Biogeography*, **6**, 49–61.

Storch, D., Keil, P. & Jetz, W. (2012) Universal species-area and endemics-area relationships at continental scales. *Nature*, **488**, 78–81.

Strong, J.S. & Leroux, S.J. (2014) Impact of non-native terrestrial mammals on the structure of the terrestrial mammal food web of Newfoundland, Canada. *PLos ONE*, **9**, e106264.

Stuessy, T.F. (2007) Evolution of specific and genetic diversity during ontogeny of island floras: The importance of understanding process for interpreting island biogeographic patterns. *Biogeography in a Changing World* (ed. by M.C. Ebach and R.S. Tangney), pp. 117–133. CRC Press, Boca Raton.

Stuessy, T.F., Jakubowsky, G., Gómez, R.S., Pfosser, M., Schlüter, P.M., Fer, T., Sun, B.-Y. & Kato, H. (2006) Anagenetic evolution in island plants. *Journal of Biogeography*, **33**, 1259–1265.

Terborgh, J. (2009) The trophic cascade on islands. *The Theory of Island Biogeography Revisited* (ed. by J.B. Losos and R.E. Ricklefs), pp. 116–142. Princeton University Press, Princeton, NJ.

Thornton, I.W.B., Zann, R.A. & van Balen, S. (1993) Colonization of Rakata (Krakatau Is.) by non-migrant land birds from 1883 to 1992 and implications for the value of island equilibrium theory. *Journal of Biogeography*, **20**, 441–452.

Tjørve, E. (2010) How to resolve the SLOSS debate: Lessons from species-diversity models. *Journal of Theoretical Biology*, **264**, 604–612.

Tscharntke, T. & Brandl, R. (2004) Plant-insect interactions in fragmented landscapes. *Annual Review of Entomology*, **49**, 405–430.

van de Crommenacker, J., Bourgeois, Y.X.C., Warren, B.H., Jackson, H., Fleischer-Dogley, F., Groombridge, J. & Bunbury, N. (2015) Using molecular tools to guide management of invasive alien species: assessing the genetic impact of a recently introduced island bird population. *Diversity and Distributions*, **21**, 1414–1427.

van der Geer, A., Lyras, G., de Vos, J. & Dermitzakis, M. (2010) Evolutionary processes in island environments. *Evolution of island mammals: adaptation and extinction of plancental mammals on islands* (ed. by A. Van Der Geer, G. Lyras, J. De Vos and M. Dermitzakis), pp. 367–389. Wiley-Blackwell, Chichester.

Wada, S., Kawakami, K. & Chiba, S. (2012) Snails can survive passage through a bird's digestive system. *Journal of Biogeography*, **39**, 69–73.

Wagner, C.E., Harmon, L.J. & Seehausen, O. (2014) Cichlid species-area relationships are shaped by adaptive radiations that scale with area. *Ecology Letters*, **17**, 583–592.

Walsh, J.C., Venter, O., Watson, J.E.M., Fuller, R.A., Blackburn, T.M. & Possingham, H.P. (2013) Exotic species richness and native species endemism increase the impact of exotic species on islands. *Global Ecology and Biogeography*, **21**, 841–850.

Wang, Y., Bao, Y., Yu, M., Xy, G. & Ding, P. (2010) Nestedness for different reasons: the distributions of birds, lizards and small mammals on islands of an inundated lake. *Diversity and Distributions*, **16**, 862–873.

Watling, J.I. & Donnelly, M.A. (2006) Fragments as islands: a synthesis of faunal responses to habitat patchiness. *Conservation Biology*, **20**, 1016–1025.

Whittaker, R.J., Bush, M.B. & Richards, K. (1989) Plant recolonization and vegetation succession on the Krakatau Islands, Indonesia. *Ecological Monographs*, **59**, 59–-123.

Wright, S.J. (1980) Density compensation in island avifaunas. *Oecologia*, **45**, 385–389.

Zalewski, M. (2004) Do smaller islands host younger populations? A case study on metapopulations of three carabid species. *Journal of Biogeography*, **31**, 1139–1148.

Table S1. Expanded version of Table 1. A non-exhaustive summary of theories, processes and patterns that a) have originated in island studies, or b) have not originated from island studies, but have received an important theoretical and/or analytical input from island studies. Examples (citations) of each theory, process or pattern are given for different types of island (see Box 1, main paper), and also for mainland systems. Many of these examples (indicated by #) are not exclusive to one particular theory, process or pattern, and could indeed also be included in one or more different sections. The main taxa used in each example are displayed in the columns. Symbols are as follows: f(x) - Theoretical study (no use, or very limited use, of empricial data); - Arthropods; - Other terrestrial invertebrates; - Mammals; - Reptiles; - Amphibians; - Birds; - Fish; - Marine invertebrates; - Plants; - Microorganisms. * indicates the studies that are part of this special issue. See main paper for references: main reference list and Appendix 1 (Data Sources).

	f(x)										
Theories/Patterns that have originated mainly from island studies											
Adaptive radiation											
Oceanic Islands											
* Algar *et al.*, this issue					X						
Blonder *et al.*, 2016										X	
Gillespie *et al.*, 2004		X									
Givnish *et al.*, 2009										X	
Grant & Grant, 2008							X				
Losos, 2011					X						
Pinto *et al.*, 2008 #					X						
Continental Islands											
Baldwin, 2007										X	
van der Geer *et al.*, 2010				X							
Habitat Islands											
Dawson & Hammer, 2005									X		
Seehausen, 2006								X			

									
Non-Island Systems									
Hughes *et al.,* 2006								X	
Pincheira-Donoso *et al.*, 2015				X					
Ecological release and Density compensation									
Oceanic Islands									
Grant & Grant, 2006						X			
Lack, 1947						X			
Novosolov *et al.*, 2016 #				X					
Schluter, 1988						X			
* Steinbauer *et al.*, this issue								X	
Wright, 1980 #						X			
Continental Islands									
Barun *et al.*, 2015			X						
Case, 1975				X					
Lomolino, 1984			X						
MacArthur, 1972						X			
Schluter & McPhail, 1992							X		
Schoener & Spiller, 1987		X		X					
Habitat Islands									
Hobbs *et al.*, 2012							X		
Martin & Pfennig, 2011					X				
McGrady-Steed & Morin, 2000									X

										
Non-Island Systems										
Adams & Rohlf, 2000					X					
Davies *et al*., 2007			X							
Schmitt & Holbrook, 1990							X			
Body size evolution and the "island rule"										
Oceanic Islands										
Clegg & Owens, 2002						X				
Lomolino, 2005 #			X	X						
Continental Islands										
Lawlor, 1982			X							
Meiri, 2007				X						
Montesinos *et al.,* 2012					X					
Habitat Islands										
Schmidt & Jensen, 2003			X							
Non-Island Systems										
McClain *et al.*, 2006								X		
Taxon cycle										
Oceanic Islands										
Economo *et al.,*, 2012		X								
Jønsson *et al.*, 2014 #						X				
Ricklefs & Bermingham, 2002				X						
Ricklefs & Cox, 1972						X				
Wilson, 1961		X								

										
Non-Island Systems										
Economo *et al.*, 2015		X								
Erwin, 1985		X								
Glazier, 1980			X							
Hoagstrom *et al.*, 2014								X		
Equilibrium Theory of Island Biogeography										
Oceanic Islands										
* Fernández-Palacios *et al.*, this issue	X									
Heaney, 2000 #			X							
MacArthur & Wilson, 1963, 1968	X									
Rosindell & Harmon, 2013 #	X									
Continental Islands										
Cody, 2006										X
Foufopoulos & Mayer, 2007							X			
Jones & Diamond, 1976							X			
Mangrove Islands										
Simberloff & Wilson, 1969, 1970		X								
Habitat Islands										
Bossard, 2014		X								
Brown, 1971, 1978			X				X			
* Dawson, this issue								X	X	
Hart & Pearson, 2011								X		
March & Bass, 1995		X								
Schoener, 1974									X	
Smith, 1979								X		

	f(x)										
Non-Island Systems											
Rosenzweig, 1975 #											
General Dynamic Model of Island Biogeography											
Oceanic Islands											
Borges & Hortal, 2009		X									
* Borregaard *et al.*, this issue	X										
Bunnefeld & Phillimore, 2012		X	X								X
Cameron *et al.*, 2013			X								
Fattorini, 2009		X	X		X	X	X				
Steinbauer *et al.*, 2013		X	X								X
Valente *et al.*, 2014	X										
Whittaker *et al.*, 2008		X	X								X
Asssembly rules, Checkerboard distributions and Null models in ecology											
Oceanic Islands											
Connor & Simberloff, 1979							X				
Connor *et al.*, 2013							X				
Diamond, 1975a							X				
Gotelli, 2000 #	X										
Mayr & Diamond, 2001							X				
* Santos *et al.*, this issue #		X									
Simberloff & Collins, 2009							X				
Continental Islands											
Cody, 2006											X

										
Habitat Islands										
Englund *et al.*, 2009										
Non-Island Systems										
Gotelli & Ellison, 2002		X								
Gotelli & Graves, 1996	X									
Gotelli *et al.*, 1997							X			
Rautenbach *et al.*, 2014				X						
Sanders *et al.*, 2007		X								
Unified Neutral Theory of Biodiversity and Biogeography										
Oceanic Islands										
Rosindell & Phillimore, 2011 [#]							X			
Continental Islands										
Hubbell, 2001, 2009										X
Habitat Islands										
Dornelas *et al.*, 2006									X	
Gilbert *et al.*, 2006										X
Non-Island Systems										
Ricklefs, 2006							X			
Rosindell *et al.*, 2015	X									

	f(x)										
Theories/patterns not originated on island systems, but that have benefited from them											
Natural Selection and Speciation											
Oceanic Islands											
Calsbeek & Cox, 2010					X						
Darwin, 1859		X	X	X	X	X	X	X	X	X	X
Grant & Grant , 2008, 2016						X					
Roderick & Gillespie, 1998		X									
Rowe *et al.*, 2016 #				X							
Savolainen *et al.*, 2006										X	
Stuessy *et al.*, 2006										X	
Continental Islands											
Clegg *et al.*, 2002 #						X					
Comes *et al.*, 2008										X	
Lescak *et al.*, 2015							X				
Habitat Islands											
Barluenga *et al.*, 2006							X				
Gao *et al.*, 2015										X	
Juan *et al.*, 2010		X	X		X		X				
Long distance dispersal and Colonization Routes											
Oceanic Islands											
Carlquist, 1966 #		X	X		X	X	X			X	
Heleno & Vargas, 2015										X	
Nathan, 2006 #										X	
Vargas *et al.*, 2012										X	
Wada *et al.*, 2012			X								

	f(x)										
Continental Islands											
Ali & Huber, 2000				X							
Alsos *et al.*, 2015										X	
Habitat Islands											
Huth *et al.*, 2015	X										
Non-Island Systems											
Bellemain & Ricklefs, 2008 #		X		X	X	X	X			X	
Brochet *et al.*, 2009										X	
Dawson & Hammer, 2008 #											X
Nicholson *et al.*, 2005 #					X						
O'Grady & DeSalle, 2008 #		X									
Patiño *et al.*, 2015 #										X	
Species-area relationship											
Oceanic Islands											
Aranda *et al.*, 2013										X	
Kisel *et al.*, 2010 #		X	X	X	X		X			X	
Lomolino & Weiser, 2001 #		X	X	X	X	X	X			X	
Losos & Schluter, 2000					X						
Ricklefs & Lovette, 1999		X		X	X	X	X				
Santos *et al.*, 2010 #		X	X	X	X	X	X			X	
Scheiner, 2003 #	X										
Triantis *et al.*, 2012 #		X	X	X	X	X	X			X	
Wright, 1983 #							X			X	

	f(x)									
Continental Islands										
Holt et al., 1999 #	X									
Kurt & Howe, 1979							X			
Panitsa *et al.*, 2006										X
Roslin *et al.*, 2014		X					X			
* Schoener et al., this issue		X			X					
Sfenthourakis, 1996		X								
Habitat Islands										
Brown & Dinsmore, 1988							X			
Belmaker *et al.*, 2007								X		
Hanski *et al.*, 2013							X			
He & Hubbel, 2011							X			X
Krauss *et al.*, 2003										
* Matthews *et al.*, this issue #		X	X	X	X	X	X			X
Newmark, 1986				X						
Wagner *et al.*, 2014								X		
Non-Island Systems										
Kisel *et al.*, 2011				X						
Qian *et al.*, 2007										X
Storch *et al.*, 2012				X		X	X			
Nestedness patterns										
Oceanic Islands										
Cook & Quinn, 1995 #		X		X	X	X	X			X
Darlington, 1957 #										
Florencio *et al.*, 2015 #		X								

										
Continental Islands										
Azeria, 2004						X				
Conroy *et al.*, 1999			X							
Dennis *et al.*, 2012		X				X				
Murakami & Hirao, 2010		X								
Wang *et al.*, 2010			X	X		X				
Habitat Islands										
Matthews *et al.*, 2015						X				
Patterson & Atmar, 1986 #			X							
Watling & Donnelly, 2006 #		X	X	X	X	X				
Non-Island Systems										
Baselga, 2010		X								
Metapopulation dynamics										
Oceanic Islands										
Farrington & Petren, 2011						X				
Garcia-Verdugo *et al.*, 2010									X	
Inchaisti & Weimerskirch, 2002 #						X				
Continental Islands										
Hanski, 2009 #		X	X			X				
Nieminen, 1996		X								
Nieminen & Hanski, 1998		X								
Zalewski, 2004		X								

											
Habitat Islands											
Bay *et al.*, 2008								X			
Hanski & Ovaskainen, 2000		X									
Non-Island Systems											
Levins, 1969, 1970	X										
Ecological Succession											
Oceanic Islands											
Edwards & Thorton, 2001		X									
Magnússon *et al.*, 2014										X	
Mueller-Dombois & Bohemer, 2013										X	
Thornton *et al.*, 1993							X				
Whitaker *et al.*, 1989										X	
Continental Islands											
Lavoie & Filion, 2001										X	
Rydin & Borgegård, 1988										X	
Mangrove Islands											
Piechnick *et al.*, 2008		X									
Habitat Islands											
McClanahan, 2014									X		
Pinotti *et al.*, 2015							X				
Non-Island Systems											
Clements, 1916										X	
Dauber & Wolters, 2005		X									
Letcher, 2010										X	

										
* Nogales *et al.*, this issue			X	X		X			X	
Olesen *et al.,* 2002		X		X					X	
* Rominger *et al.*, this issue		X								
* Traveset *et al.*, this issue [#]		X		X		X			X	
Continental Islands										
Strong & Leroux, 2014			X							
Terborgh, 2009 [#]		X	X	X	X	X				
Terborgh *et al.*, 2001		X	X	X	X	X				
Mangrove Islands										
* Cirtwill & Stouffer, this issue		X							X	
Gravel *et al.*, 2011 [#]	X	X					X	X		X
Habitat Islands										
Harvey & MacDougall, 2014		X							X	
Holt, 2009 [#]		X	X			X				
Tscharntke & Brandl, 2004		X							X	
Non-Island Systems										
Amaresakare, 2008										
Pimm, 1982										

	f(x)										
Conservation Theory - Invasive species, Extinction and Habitat fragmentation											
Oceanic Islands											
Bellard *et al.*, 2014 #				X	X	X	X	X		X	
* Blackburn *et al.*, this issue #							X			X	
Boyer *et al.*, 2014 #							X				
Coblentz, 1978 #				X						X	
Duncan *et al.*, 2013 #							X				
Kueffer *et al.*, 2010 #										X	
Sax *et al.*, 2002 #							X			X	
Triantis *et al.*, 2010		X									
Walsh *et al.*, 2013 #				X		X	X				
Continental Islands											
Gasc *et al.*, 2010				X	X						
Pattermore & Wilcove, 2012				X			X				
Pretto *et al.*, 2012										X	
van de Crommenacker *et al.*, 2015		X					X				
Habitat Islands											
Diamond, 1975b, 1981											
Krauss *et al.*, 2010		X								X	
Larsen *et al.*, 2005 #											
Laurence, 2009											
Lindenmayer, 2015							X				
Simberlogg & Abele, 1976											
Tjørve, 2010	X										